

The snakeflies of the Mediterranean islands: review and biogeographical analysis (Neuropterida, Raphidioptera)

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Abstract

The Mediterranean region represents one of the hotspots of biodiversity of many organisms and among these also of Raphidioptera. With about 250 known species world-wide Raphidioptera is the smallest order of extant holometabolous insects.

The Mediterranean region harbors 113 species (= >45% of the world fauna), and of these 33 (= >13% of the world fauna) have been found on islands of the Mediterranean Sea. In the course of the past 50 years most of the larger islands have been intensively explored for Raphidioptera, particularly all islands (except the Balears) which had no connection to the mainland throughout the whole Pleistocene. Altogether, 11 species of Raphidioptera (9 Raphidiidae, 2 Inocelliidae) are endemic to (usually) one, rarely to a few Mediterranean islands:

Phaeostigma (Ph.) *euboica* (Euboea), *Ph. (Aegeoraphidia) prophetica* (Rhodes), *Ph. (Ae.) karpethana* (Karpethos), *Ph. (Ae.) biroi* (Crete), *Ph. (Superboraphidia) minois* (Crete), *Subilla principiae* (Sardinia), *S. colossea* (Rhodes), *Raphidia* (R.) *peterressli* (Chios), *R. (R.) ariadne* (Crete), *Fibla* (F.) *maclachlani* (Corsica, Sardinia, Sicily), *F. (Reisserella) pasiphae* (Crete).

In the Aegean Sea there is a remarkable difference between the eastern and the western islands marked by the so-called Rechinger line based on results of the analysis of the flora. The Raphidioptera confirm this line impressively.

It is rather unlikely that further Raphidioptera species endemic to Mediterranean islands are still to be detected – with one exception: the Balears. A few additional species known from various parts of the continents surrounding the Mediterranean Sea will probably be found on islands so that a total number may be around 40, possibly around 45 species.

The possible ways and times of colonization of the islands by Raphidioptera are discussed. The present paper may serve as a basis for studies on natural and particularly on anthropogenic dispersals of snakeflies from island to island, from mainland to islands, and from islands to the mainland in connection with phylogeographic investigations.

Key Words

colonization of islands, dispersal to and from islands, endemic species, Inocelliidae, Mediterranean region, Pleistocene, Raphidiidae, Rechinger line, refugial centers

Introduction

Raphidioptera

The Raphidioptera (snakeflies) is the smallest order of holometabolous insects. So far ca. 250 described valid species are known, and although several species are still to be detect-

ed, it is very unlikely that the real number of snakefly species harboring our planet presently exceeds 300. The order comprises two families: Raphidiidae (with ca. 210 known species) and Inocelliidae (with > 40 species). The two families have a similar general appearance, but are easily distinguished by several striking features. All snakeflies are characterized by an elongated prothorax, by translucent wings

with a sparse wing venation and a pterostigma, by a great variety of the genital sclerites, particularly in males, and by a conspicuous ovipositor of the females (e.g. Fig. 2a, b).

Both families are characterized by long developmental periods. Most species need two years with at least one hibernation of the mature larva (or rarely pupa). The larvae of the majority of species (many Raphidiidae and probably all Inocelliidae) (e.g. Figs 2c, 6h) are corticolous, but larvae of many species of Raphidiidae live in the detritus around roots of bushes or in crevices of rocks. Larvae of all snakeflies and adults of the Raphidiidae are predators of various soft-bodied arthropods, while adults of Inocelliidae feed (at least sometimes) on pollen. All adult snakeflies are active in the day-time; very rarely single specimens are exceptionally attracted by artificial light.

Today, the distribution of both families of the order is confined to arboreal parts of the Northern Hemisphere (Fig. 1), which is to be traced back to the fact that a decrease of temperature during winter is a precondition for a normal development (H. Aspöck and U. Aspöck 1991; H. Aspöck 2002; H. Aspöck et al. 2018, 2019). In the Mesozoic, particularly in the Cretaceous, snakeflies had their Golden Age. Probably the planet was inhabited by thousands of species, and Raphidioptera occurred also in tropical zones and the Southern Hemisphere. At the end of the Cretaceous, about 66 million years ago (mya), an asteroid of more than 10 km diameter crashed into the earth causing a worldwide darkness and a decrease of temperature for several years. This dramatic change in all terrestrial ecosystems probably led to the near extinction of the snakeflies; however, at least two lines survived in the Northern Hemisphere representing the two families of our times. Their general appearance resembles largely that of the Mesozoic Raphidioptera (H. As-

pöck 1998; Lu et al. 2020). The extant Raphidioptera may be justifiably apostrophized as living fossils.

Most snakefly species are characterized by small, in many cases extremely small distribution areas largely restricted to glacial or postglacial refugial areas. The capacity to disperse and thus their expansivity are usually very low; there are only very few species with large distributions, e.g. from Central Europe to the Far East. These species have apparently several or even many scattered refugial areas from which they have spread.

These chorological and biogeographical characteristics are also of striking significance for an understanding of the Raphidioptera fauna of the Mediterranean islands.

Monographs and overviews on Raphidioptera: H. Aspöck et al. (1991), H. Aspöck et al. (2001), H. Aspöck and U. Aspöck (2009), U. Aspöck and H. Aspöck (2009).

The islands of the Mediterranean Sea

The Mediterranean Sea is the remnant of the ancient Tethys Ocean and today restricted to an area of about 2.1 million km² between Europe, Asia, and Africa. It is connected with the Atlantic Ocean through the Strait of Gibraltar. At the end of the Miocene, in the Messinian, about 6 mya, the connection to the Atlantic Ocean was closed due to tectonic events. This led to the so-called Messinian salinity crisis and to the evaporation of the Mediterranean Sea. Between about 6 and 5 mya closing and opening of the Strait of Gibraltar happened several times (Hofrichter 2020).

Presently, there are more than 4,300 islands in the Mediterranean Sea, most of them small and uninhabited, in many cases only rocks. However, some islands are large (e.g.

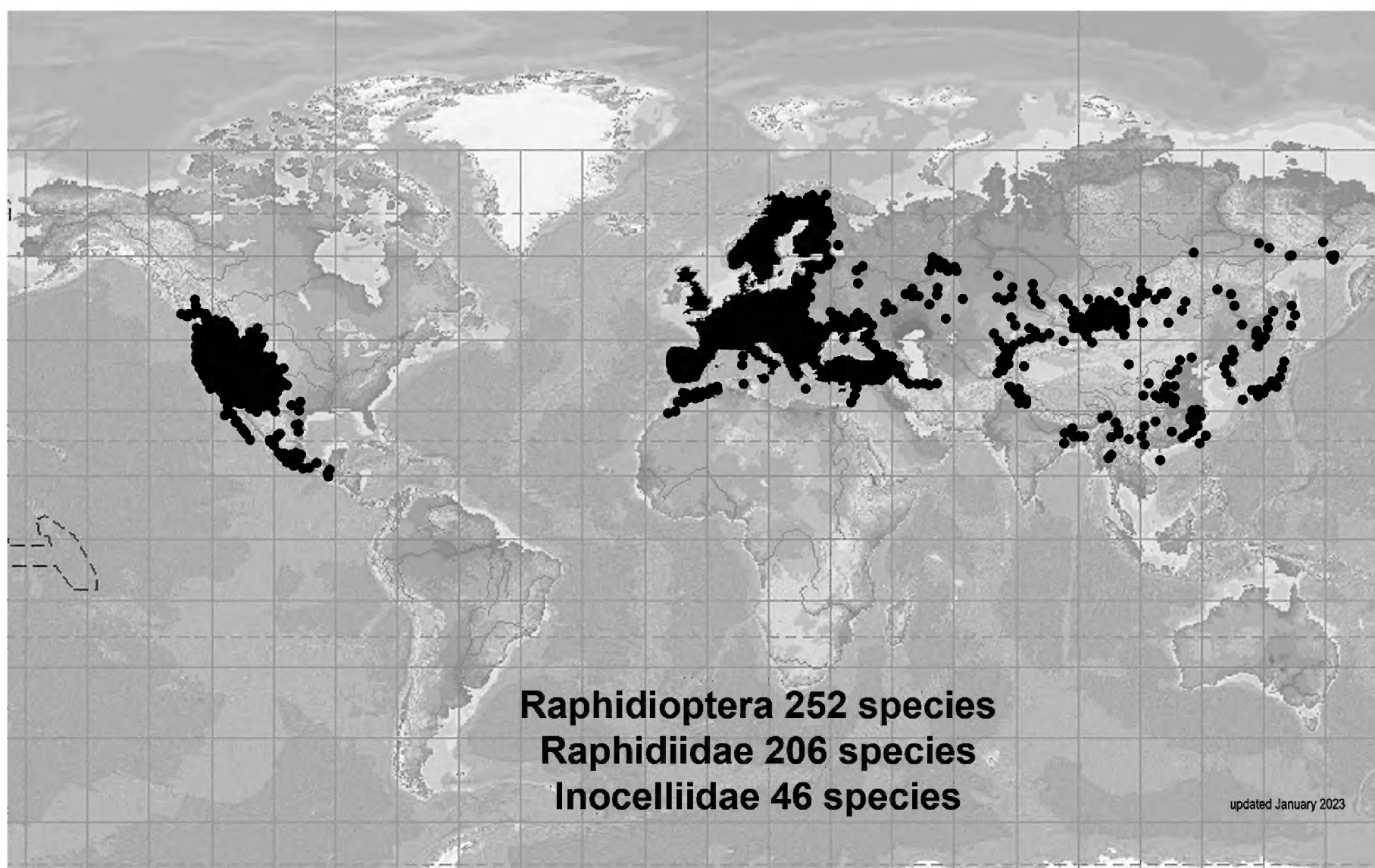


Figure 1. World distribution of Raphidioptera.

Sicily with more than 25,000 km², Sardinia with more than 24,000 km², eight islands with sizes of 1,000 km² to almost 10,000 km², and many of sizes of several hundred km²). Several islands have high elevations (e.g. Sicily >3300 m, Sardinia >1800 m, Corsica >2700 m, Euboea >1700 m, Crete >2450 m, Rhodes 1250 m, Cyprus >1950 m) with large forests and thus excellent ecological conditions for snakeflies.

The genesis of the islands is very different. Some of them represent fragments broken off from the margins of the continent and drifted into the sea, e.g. Sardinia, Corsica, and the Balears broke off from Iberia in the Oligocene, between 35 and 28 mya. Others represent the exposed elevations of otherwise flooded parts of adjacent continental areas. Crete is a good example: The island is the southernmost part of Europe in the Eastern Mediterranean. Originally the whole Aegean was land, due to subsequent tectonic events extensive transgressions occurred, which led to the Aegean Sea in the Miocene, about 15 mya. Crete remained as an island (Simaiakis and Mylonas 2008).

Sicily is an island composed of three parts of different origin. The northeasternmost part comes from the Apennine Peninsula (which consists of the Apennines on one hand and the Apulian Plate on the other hand). The northwestern part of Sicily (including central parts) derives from Iberia, namely from the land broken off from the continent in the Oligocene. The south of Sicily is of African origin (Rögl, pers. comm.).

Cyprus is derived from the Levantine mainland, the submarine separation occurred probably in the Miocene. This separated part drifted to the west and emerged from the sea later (Rögl, pers. comm., Badano and Makris 2020).

Rhodes was once a part of Anatolia and became separated possibly in the Pliocene due to tectonic events and subsequent transgressions (Rögl et al. 1991; Simaiakis and Mylonas 2008).

Most of the islands near the mainland had connections to the mainland during the glacial periods of the Pleistocene, when the sea level was up to 230 m lower than today, so that an exchange of the faunas was possible. A few islands remained, however, isolated or only connected with neighboring islands, but not with the mainland. Sardinia and Corsica (Corsardinia) were sometimes connected to each other, but never to the mainland since their separation from Iberia. Crete was affected by several transgressions, but at no time was the whole island flooded; some parts always remained as islands. There were no land bridges to the European or the African mainland since the appearance of Crete in the Miocene. Neither Cyprus nor Rhodes had connections to the mainland, at least not in the Pleistocene.

Long isolation of an island from the mainland is an important precondition for the evolution of endemic species restricted to a certain island. As regards the Raphidioptera of Mediterranean islands, Sardinia, Corsica, Crete, Karpathos, and Rhodes do harbor endemic snakeflies, and none of these islands had any connection to continental regions at least throughout the whole Pleistocene. Euboea also harbors at least one endemic snakefly, but this is due to a refugial center in high mountains (see Dis-

cussion). Interestingly, Cyprus has no endemic snakefly. So far, the order Raphidioptera has not yet been recorded from the Balears. However, it is out of the question for snakeflies to occur on these islands, at least on Mallorca with elevations almost up to 1,500 m. See also chapter 4.3.2 on endemic species.

History of research on Raphidioptera of the islands of the Mediterranean

The first record of a snakefly from Mediterranean islands dates back to Dominicus Scina (1818), who listed “*Raphidia ophiopsis*” among the insects of Palermo. *Raphidia ophiopsis* does not occur in Sicily, so we do not know which species he had really found. At that time almost every snakefly was called “*Raphidia ophiopsis*”. Hagen (1867) was the first one who published reliable records of Raphidioptera from Mediterranean islands. He described *Raphidia corsica* (today: *Xanthostigma corsica*) from Corsica and *Raphidia cyprica* (today: *Phaeostigma (Crassoraphidia) cyprica*) from Cyprus. This is a small and short paper; nevertheless it is a milestone in raphidiopterology (and even in entomology in general) as it contains descriptions of five new species solely based on characters of the male genitalia. More than 20 years passed until the next record of a snakefly on a Mediterranean island was published: Novak (1891) recorded *Raphidia affinis* Schneider (today: *Dichrostigma flavipes*) from the Adriatic island Hvar. The first record of a species of the family Inocelliidae was published by Albarda (1891) in his admirable “Révision des Rhaphidides”. He described *Inocellia maclachlani* (today: *Fibla (F.) maclachlani*) from Corsica. The first record of a snakefly on Crete was published by Navás (1915a), when he described *Lesna biroi* (today: *Phaeostigma (Aegeoraphidia) biroi*), a species endemic to Crete. No further discoveries of snakeflies on Mediterranean islands were made during the following decades. In 1960, only three species of Raphidiidae and one species of Inocelliidae were known from a total of four Mediterranean islands: Corsica, Hvar, Crete, and Cyprus. In the first half of the 1960s we began an intensive work on Raphidioptera. A study of the large collection of unidentified snakeflies of the Natural History Museum Vienna (and of other collections) led to descriptions of a second snakefly species from Crete – *Raphidia ariadne* – and of the first snakefly species – *Phaeostigma (Aegeoraphidia) prophetica* – from Rhodes (H. Aspöck and U. Aspöck 1964a, 1965a). Moreover, a female of an unknown species of Inocelliidae from Crete was described and figured (but not named), which represented the first record of this family on an Aegean island. A few years later a male of this species was found so that the species could adequately be described (H. Aspöck and U. Aspöck 1971b): *Fibla (Reisserella) pasiphae*. From 1966 onwards we explored regularly and systematically the Raphidioptera fauna of the Mediterranean region, and from 1973 onwards particularly also that of the islands (Naxos, Syros, Chios, Samos, Ikaria,

Euboea, Thasos, Samothraki, Skopelos, Skyros, Levkas, Rhodes, Sicily, Crete, Karpathos, Lesbos, Limnos, Cyprus, Sardinia, Corsica; for details see Gusenleitner 2004; H. Rausch and R. Rausch 2004; H. Aspöck 2012). These field trips led to discoveries of new species or subspecies: *Phaeostigma* (Ph.) *euboica*, Ph. (*Graecoraphidia*) *divina retsinata*, *Phaeostigma* (*Magnoraphidia*) *flammi*, Ph. (*Pontoraphidia*) *setulosa aegea*, Ph. (*Aegeoraphidia*) *karpathana*, Ph. (*Superboraphidia*) *minois*, *Subilla prinicipiae*, *S. colossea*, *Raphidia* (R.) *mediterranea*, *Raphidia* (R.) *peterressli*, *Fibla* (*Reisserella*) *pasiphae* (H. Aspöck and U. Aspöck 1971b, 1973, 1976; H. Aspöck et al. 1977, 1979, 1991; U. Aspöck and H. Aspöck 1989, 1990; Pantaleoni et al. 2005).

In addition, several species known from mainland regions were found on Mediterranean islands for the first time: *Venustoraphidia nigricollis*, *Parvoraphidia microstigma*, *Ornatoraphidia flavilabris*, *O. christianodagmara*, *Phaeostigma* (*Magnoraphidia*) *major*, Ph. (M.) *wewalkai*, Ph. (*Aegeoraphidia*) *raddai*, *Subilla confinis*, *S. artemis*, *Ulrike syriaca*, *R. (R.) beieri*, *R. (R.) mysia*, *R. (R.) ambigua*, *Parainocellia ressi*.

During the past fifteen years no new species have been found on any of the islands, and only further records of known species were made. Thus, the time has come to review the present state of knowledge and to analyze the genesis of the composition of the snakefly fauna of the Mediterranean islands.

Materials and methods

This comprehensive review and overview is based on several thousand specimens of Raphidioptera from Mediterranean islands identified by us over the past 60 years. Many of these studies – particularly all descriptions of new taxa – were published in many papers scattered in many journals. All publications on Raphidioptera which appeared before 1991 have been considered and cited in our monograph (Aspöck et al. 1991), and except original descriptions these papers are not dealt with here again. However, all publications from 1991 onwards dealing with species on Mediterranean islands are considered here and are listed in the synonymy lists of each taxon. Large parts of specimens of Raphidioptera of the Mediterranean regions including the islands are deposited in the following collections: Naturhistorisches Museum Wien, Biologiezentrum Linz, private collection Horst and Ulrike Aspöck (Vienna), private collection Hubert and Renate Rausch (Scheibbs, Lower Austria). Further specimens of Raphidioptera from Mediterranean islands are deposited in most European museums; we have seen and identified by far the largest part of these (see Aspöck et al. 1991).

The maps showing the distribution of Raphidioptera on Mediterranean islands were provided with ArcGIS/ArcMap ver. 10.3.1.4959. Source of the map: National Geographic-Weltkarte – Content may not reflect National Geographic's current map policy. Sources: National Geographic, ESRI, DeLorme, HERE, UNEP-WCMC, USGS,

NASA, ESA, METI, NRCAN, GEBCO, NOAA, increment P Corp.

The systematic order follows H. Aspöck and U. Aspöck (2014). For details see also H. Aspöck et al. (1991, 2001), U. Aspöck and H. Aspöck (1989, 1990), Pantaleoni et al. (2005).

Abbreviations used in the synonymy lists: **anat** = anatomy; **anncat** = annotated catalogue; **asl** = above sea level; **bibliogr** = bibliography; **biogeogr** = biogeography; **biol** = biology; **cat** = catalogue; **charact** = characterization; **chorol** = chorology; **com** = comment; **comp-morph** = comparative morphology; **descr** = description; **distr** = distribution; **distrmap** = distribution map; **ecol** = ecology; **ethol**: **cop** = ethology, copulation; **etymol** = etymology; **FD!** = false determination; **gs** = genital segments; **ill** = illustration; **imag** = imago (adult); **la** = larva; **list** = listed; **molecsyst** = molecular systematics; **mon** = monograph; **nom** = nomenclature; **odescr** = original description; **overv** = overview; **paras** = parasites, parasitoids; **phyl** = phylogeny; **phylogeogr** = phylogeography; **phyltree** = phylogenetic tree; **pu** = pupa; **rec** = record; **s.l.** = sensu lato; **s. str.** = sensu stricto; **synlist** = synonymy list; **syst** = systematics; **tax** = taxonomy

An annotated catalogue of the Raphidioptera of the Mediterranean islands with comments on the systematics, taxonomy, biology, ecology, chorology and biogeography

In the following, the 33 species of Raphidioptera recorded from Mediterranean islands are treated with respect to their synonymies, taxonomy, systematics, biology, ecology, distribution, and biogeography (Tables 1, 2).

Family Raphidiidae Latreille, 1810

Family Raphidiidae Latreille, 1810: H. Aspöck et al. 1991 (mon); H. Aspöck and U. Aspöck 1991 (overv); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol); H. Aspöck and U. Aspöck 2009 (overv); U. Aspöck and H. Aspöck 2009 (overv); Haring et al. 2011 (phylogeny); Oswald and Machado 2018 (overv); Gruppe et al. 2023 (biol).

Venustoraphidia H. Aspöck & U. Aspöck, 1968

Venustoraphidia H. Aspöck & U. Aspöck, 1968 (odescr) (described as a subgenus of *Raphidia* L.) [type species by original designation: *Raphidia nigricollis* Albarda, 1891]: H. Aspöck et al. 1991 (mon); H. Aspöck et al. 1989 (biogeogr, distr, ill: distrmap); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol, paras); Haring et al. 2011 (phyl); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat); Monserrat and Papenberg 2012, 2015 (mon).

Table 1. Records of Raphidioptera on Mediterranean islands I.

	Corsica	Sardinia	Sicily	Elba	Giglio	Krk	Hvar	Corfu	Levkas	Kefalonia	Thasos	Samothrace	Skopelos	Skyros	Euboea	Andros	Aegina	Hydra	Naxos	Paros	Crete	Karpathos	Lesbos	Samos	Icaria	Chios	Rhodos	Cyprus
Raphidiidae																												
<i>Vemustoraphidia</i>											x																	
<i>V. nigricollis</i>											x																	
<i>Xanthostigma</i>	x	x	x	x	x																							
<i>X. corsica</i>	x	x	x	x	x																							
<i>X. aloysiana</i>		x																										
<i>Parvoraphidia</i>									x																			
<i>P. microstigma</i>									x																			
<i>Ornatoraphidia</i>									x						x													
<i>O. flavilabris</i>									x																			
<i>O. christianodagmara</i>															x													
<i>Phaeostigma</i>									x	x	x		x		x						x	x	x	x	x	x	x	x
<i>Phaeostigma</i> s.str.															x													
<i>Ph. (Ph.) euboica</i>															x													
<i>Graecoraphidia</i>															x													
<i>Ph. (G.) divina retsinata</i>															x													
<i>Crassoraphidia</i>																												x
<i>Ph. (C.) cyprica</i>																												x
<i>Magnoraphidia</i>									x	x			x		x													
<i>Ph. (M.) major</i>									x	x																		
<i>Ph. (M.) flammi</i>													x		x													
<i>Ph. (M.) wewalkai</i>															x													
<i>Pontoraphidia</i>											x																	
<i>Ph. (P.) setulosa aegea</i>											x																	
<i>Aegeoraphidia</i>																					x	x	x	x	x	x	x	
<i>Ph. (Ae.) raddai</i>																							x	x	x	x		
<i>Ph. (Ae.) prophetica</i>																											x	
<i>Ph. (Ae.) karpathana</i>																						x						
<i>Ph. (Ae.) biroi</i>																					x							
<i>Superboraphidia</i>																					x							
<i>Ph. (S.) minois</i>																					x							

Table 2. Records of Raphidioptera on Mediterranean islands II.

	Corsica	Sardinia	Sicily	Elba	Giglio	Krk	Hvar	Corfu	Levkas	Kefalonia	Thasos	Samothrace	Skopelos	Skyros	Euboea	Andros	Aegina	Hydra	Naxos	Paros	Crete	Karpathos	Lesbos	Samos	Icaria	Chios	Rhodos	Cyprus
<i>Subilla</i>		x	x						x																		x	
<i>S. confinis</i>			x																									
<i>S. artemis</i>									x																			
<i>S. principiae</i>		x																										
<i>S. colossea</i>																											x	
<i>Ulrike</i>																												x
<i>U. syriaca</i>																												x
<i>Raphidia</i>											x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Raphidia</i> s.str.											x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>R. (R.) mediterranea</i>														x	x	x	x	x	x	x		x			x			
<i>R. (R.) beieri</i>											x	x				x	x	x	x	x								
<i>R. (R.) peterressli</i>																										x		
<i>R. (R.) mysia</i>																							x					
<i>R. (R.) ambigua</i>																								x			x	
<i>R. (R.) ariadne</i>																					x							
<i>Dichrostigma</i>						x	x	x																				
<i>D. flavipes</i>						x	x	x																				
Inocelliidae																												
<i>Fibla</i>	x	x	x																			x						
<i>Fibla</i> s.str.	x	x	x																									
<i>F. (F.) maclachlani</i>	x	x	x																									
<i>Reisserella</i>																						x						
<i>F. (R.) pasiphae</i>																					x							
<i>Parainocellia</i>																								x				
<i>P. resli</i>																								x				

Taxonomy and systematics. H. Aspöck et al. (1991), Haring et al. (2011), Monserrat and Papenberg (2012, 2015). The genus is markedly differentiated by morphological characters of adults and larvae and also by molecular phylogeny. It has emerged as the sister group of (*Puncha* + *Calabroraphidia*) + *Xanthostigma*. *Venustoraphidia* comprises three geographically vicariant species.

Biology and ecology. Larvae corticolous on a great variety of deciduous and coniferous trees. Development usually two years. Last hibernation stage: full-grown larva. Adults: (EIV)V–VI(BVII).

Distribution. Apennine Peninsula, Balkan Peninsula, northern part of Iberian Peninsula, Central and Eastern Europe.

Venustoraphidia nigricollis (Albarda, 1891)

Raphidia nigricollis Albarda, 1891 (odescr): H. Aspöck et al. 1991 (mon). *Venustoraphidia nigricollis* (Albarda 1891): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Pantaleoni 1990b (ecol); Pantaleoni 1990d [1993] (rec); Kielhorn 1991 (ecol, rec); Saure and Gerstberger 1991 (ecol, rec); Devetak 1992a (rec); Devetak 1995 (rec); Pröse 1995 (distr, rec); H. Aspöck and Hölzel 1996 (distr); Saure 1996 (biogeogr, ecol, rec); Sziráki 1996 (ecol, rec); Achtelig 1997 (ecol, rec); Gruppe 1997 (ecol, rec); Schubert and Gruppe 1999 (ecol, rec); Sziráki 1999 (rec); H. Aspöck et al. 2001 (anncat); Gruppe and Schubert 2001 (ecol, rec); Tröger 2002 (rec); Popov 2004 (chorol); Gruppe 2006a (ecol); Gruppe 2006b (ecol, rec); H. Aspöck and U. Aspöck 2007 (biogeogr, distr); Pantaleoni 2007 (biol); Gruppe 2008 (ecol, rec); Klokočovník et al. 2010 (rec); Letardi et al. 2010 (rec); H. Aspöck and U. Aspöck 2013 (cat, etymol); H. Aspöck and U. Aspöck 2014 (cat); Weissmair et al. 2021 (biol, ecol); H. Aspöck and U. Aspöck 2021 (overv, ill: la, pu, ♂, ♀ imag), 2022a (overv, ill: la, pu, ♂, ♀ imag), 2022b (overv, ill: la, pu, ♂, ♀ imag); Tillier et al. 2022b (rec).

Taxonomy. H. Aspöck et al. (1991). Adults can easily be identified by the entirely black pronotum, usually already by the small size (Fig. 2a, b). Larvae are readily recognizable by the characteristic pattern of the dorsal pigmentation (Fig. 2c).

Biology and ecology. Larvae exclusively corticolous on *Quercus*, *Malus*, *Pyrus*, *Acer* and many other deciduous trees, but also on *Pinus* in light forests and in wild gardens and even in urban parks in altitudes up to ca. 500 m (Central Europe), records in Southern Europe 700 to 1100 m. Development at least two years. Last hibernating stage: full-grown larva. Adults: V–VII.

Records on Mediterranean islands (Fig. 7b). Thasos (Ipsarion, ca. 1000 m, on *Pinus*). Syntopic Raphidioptera on Thasos: *Phaeostigma* (*Pontoraphidia*) *setulosa aegea*, *Raphidia* (*R.*) *beieri*.

Continental distribution. Balkan Peninsula as far south as to the gulf of Korinthos, Eastern Europe, Apennine Peninsula (Northern Italy, Calabria), Central Europe as far north as to Northern Germany, Eastern and Southern France.

Biogeography. Polycentric Adriato-Balkanopontomediterranean faunal element with high expansivity.

Xanthostigma Navás, 1909

Xanthostigma Navás, 1909 (described as a section of *Raphidia* L.) [type species by absolute tautonymy: *Raphidia xanthostigma* Schummel, 1832]: H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 1999 (ecol, chorol); H. Aspöck 2002 (biol, paras); H. Aspöck et al. 2001 (anncat); Haring et al. 2011 (phyl); U. Aspöck et al. 2012 (fig: phyltree, list); H. Aspöck and U. Aspöck 2013 (cat, etymol, phyl), 2014 (cat); Monserrat and Papenberg 2015 (overv). *Raphidilla* Navás, 1915b [type species by original designation: *Raphidia xanthostigma* Schummel, 1832]: H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom). *Rhaphidilla* Navás, [1919] 1918b [unjustified emendation of *Raphidilla* Navás, 1915]: H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck and U. Aspöck 2014 (cat).

Taxonomy and systematics. H. Aspöck et al. (1991), Haring et al. (2011). *Xanthostigma* is a morphologically clearly differentiated genus of the *Puncha* clade and according to molecular phylogeny results is the sister taxon of *Puncha* + *Calabroraphidia* or of *Italoraphidia*. The genus comprises five known species with very different distribution patterns including Eurosibirian, Mongolian, Pontocaspian, and Mediterranean faunal elements.

Biology and ecology. Larvae of *X. corsica* probably mainly in upper layers of soil, but also corticolous (*Quercus*, *Pinus*). Larvae of *X. xanthostigma* (probably strictly) corticolous on a great variety of deciduous as well as of coniferous trees. Substrate of larvae of other species unknown. Development – as far as known – usually two years. Last hibernation stage: full-grown larva. Adults: IV–VII.

Distribution. Almost whole of Europe from southernmost parts (*X. corsica*) to northern parts of Scandinavia over the North of Asia as far as to Far East (*X. xanthostigma*). Caucasus region, Mongolia, northern China.

Xanthostigma corsica (Hagen, 1867)

Raphidia corsica Hagen, 1867 (odescr): H. Aspöck et al. 1991 (mon). *Raphidia insularis* Albarda, 1891 (odescr): H. Aspöck et al. 1991 (mon). *Puncha italica* Navás, 1927b (odescr): H. Aspöck et al. 1991 (mon). *Xanthostigma corsica* (Hagen, 1867): H. Aspöck et al. 1991 (mon); Pantaleoni 1990c (com, rec); H. Aspöck and Hölzel 1996 (distr); Letardi and Pantaleoni 1996 (rec); H. Aspöck et al. 2001 (anncat); Letardi and Maltzeff 2001 (rec); Nicoli Aldini and Baviera 2001 (rec); H. Aspöck and U. Aspöck 2007 (biogeogr, distr); Letardi et al. 2008 (list, rec); Badano and Letardi 2010 (rec); Haring et al. 2011 (phyl, phyltree); Nicoli Aldini et al. 2012 (rec, distr); H. Aspöck and U. Aspöck 2013 (cat, etymol; ill: imag, la), 2014 (cat). *Xanthostigma corsicum* (Hagen): Monserrat and Papenberg 2015 (mon, rec, synlist); Tillier et al. 2022a (rec).

Taxonomy. H. Aspöck et al. (1991), Monserrat and Papenberg (2015). *X. corsica* can always easily be identified by morphological characters (e.g. three cells between R and Rs in forewing) (Fig. 2d).

Biology and ecology. Larvae mainly terricolous, however, several records also under bark of *Pinus* and of *Quercus*. Many records of adults mainly on low vegetation and on bushes (particularly *Genista*) in a great variety of different biotops: light oak and/or pine forests, various kinds of light mixed forests with a rich bush vegetation from sea level to 1500 m. Development usually two years. Last hibernation stage: full-grown larva. Adults: IV–VII.

Records on Mediterranean islands (Fig. 8a). *X. corsica* is a frequent snakefly in various biotopes in altitudes from 0 to 1500 m asl on Sicily, Sardinia, Corsica, Giglio and Elba. Probably it occurs also on several smaller Mediterranean islands west of the mainland of Italy. Syntopic Raphidioptera: *Xanthostigma aloysiana* (Sardinia), *Subilla confinis* (Sicily), *Fibla maclachlani* (Sicily, Sardinia, Corsica).

Continental distribution. The species occurs on the Apennine Peninsula from the south of Calabria to Tuscany in the north; moreover it has been recorded in the south of France and the west of Spain. It is possible that the western populations are remnants of a very old invasion and might be differentiated phylogenomically from the Eastern populations. The populations on the Italian islands and on Corsica seem to be rather homogenous. One may assume that this rather frequent species is more or less regularly transferred by anthropogenic activities from the mainland or from one island to another.

Biogeography. Polycentric Tyrrhenic-Adriato-Atlantomediterranean faunal element.

Xanthostigma aloysiana (Costa, 1855)

Raphidia aloysiana Costa, 1855 (odescr): H. Aspöck et al. 1991 (mon). *Raphidilla puella* Navás, 1915c (odescr): H. Aspöck et al. 1991 (mon); H. Aspöck and U. Aspöck 2014 (cat).

Raphidilla soror Navás, 1915c (odescr): H. Aspöck et al. 1991 (mon); H. Aspöck and U. Aspöck 2014 (cat).

Xanthostigma aloysiana (Costa): H. Aspöck et al. 1991 (mon); H. Aspöck and Hölzel 1996 (distr); Letardi and Pantaleoni 1996 (rec); Monserrat 1996 (distr); H. Aspöck et al. 2001 (anncat); U. Aspöck and H. Aspöck 2005b (biogeogr); Pantaleoni 2005 (rec); H. Aspöck and U. Aspöck 2007 (biogeogr, distr); Badano 2008 (distr, rec); Badano and Letardi 2010 (rec); Monserrat and Papenberg 2010 (chorol); Haring et al. 2011 (phyl, phyltree); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Xanthostigma aloysianum (Costa): Letardi and Maltzeff 2008; Letardi 2015 (rec); Monserrat and Papenberg 2015 (mon, rec, synlist); Thierry et al. 2021 (rec, distr).

Taxonomy. H. Aspöck et al. 1991 (mon). *X. aloysiana* resembles superficially *X. corsica*, but can easily be differentiated by eidonomic characters (e.g. only two cells between R and Rs in the forewing).

Biology and ecology. Poorly known. Larvae probably terricolous. Adults in light pine forests or light mixed forests with rich bush vegetation and in macchias of different structure in altitudes of 600 to 1200 m, usually found in single specimens only. Adults: V–VII.

Records on Mediterranean islands (Fig. 8a). So far only in Central Sardinia (Gennargentu). These findings, so far not properly published, are from altitudes slightly below 1000 m. Syntopic Raphidioptera in Sardinia: *Xanthostigma corsica*, *Fibla maclachlani*.

Continental distribution. Records in all major parts of the Apennine Peninsula, in the south of Switzerland, southern France, and in the northeast of Spain in altitudes between 600 and 1200 m.

Biogeography. Monocentric Adriatomediterranean faunal element with moderate expansivity.

Parvoraphidia H. Aspöck & U. Aspöck, 1968

Parvoraphidia H. Aspöck & U. Aspöck, 1968 (odescr) (described as a subgenus of *Raphidia* L.) [type species by original designation: *Raphidia microstigma* Stein, 1863]: H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol); U. Aspöck and H. Aspöck 2005b (com); Haring et al. 2011 (phyl); H. Aspöck 2012 (cat); U. Aspöck et al. 2012 (fig: phyltree; list); H. Aspöck and U. Aspöck 2013 (cat, etymol, phyl); H. Aspöck and U. Aspöck 2014 (cat).

Taxonomy and systematics. H. Aspöck et al. (1991), Haring et al. (2011). *Parvoraphidia* is markedly differentiated by morphological characters of adults (small size: 5–8,5 mm; short and very dark pterostigma) (Fig. 2f) and larvae and also by molecular phylogeny. It has emerged as the sister group of *Ornatoraphidia* + *Turcoraphidia*, the genus comprises three closely related species (including one subspecies), which can be reliably differentiated only by characters of the male genitalia.

Biology and ecology. The larvae of all species of the genus live in upper layers of soil. Development probably (mainly) one year. Last stage of hibernation: (probably) full-grown larva.

Distribution. *Parvoraphidia* is confined to the southern and southwestern parts of the Balkan Peninsula.

Biogeography. The three species represent Balkanopontomediterranean faunal elements with low expansivity.

Parvoraphidia microstigma (Stein, 1863)

Raphidia microstigma Stein, 1863 (odescr): H. Aspöck et al. 1991 (mon); H. Aspöck and U. Aspöck 2014 (cat).

Raphidia (*Parvoraphidia*) *microstigma* Stein: H. Aspöck et al. 1991 (mon).

Parvoraphidia microstigma (Stein, 1863): H. Aspöck et al. 1991 (mon); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); Haring et al. 2011 (phyl, phyltree); H. Aspöck and U. Aspöck 2013 (cat, etymol; ill: imag), 2014 (cat); Sziráki 2014 (rec).

Taxonomy. H. Aspöck et al. (1991). *P. microstigma* can be morphologically differentiated only by characters of the male genitalia, however, the three species (and one subspecies) of the genus show perfect geographical vicariance.

Biology and ecology. Larvae probably exclusively ter-ricolous. Numerous records of adults on low vegetation, bushes and trees in various habitats: light oak and pine forests, on clearings within fir tree forests, on slopes with *Genista*, on hedgerows at fields in altitudes of 650–1200 m. Development possibly only one year. Last hibernation stage: probably full-grown larva. Adults: V–VII.

Records on Mediterranean islands (Fig. 7b). Records so far only on Levkas. It is, however, likely that the species will also be found on other Ionian islands. Syntopic Raphidioptera on Levkas: *Ornatoraphidia flavilabris*, *Phaeostigma* (*Magnoraphidia*) *major*, *Subilla artemis*.

Continental distribution. Greece north of the gulf of Korinthos, Albania, North Macedonia.

Biogeography. Stationary monocentric Balkanopontomediterranean faunal element.

Ornatoraphidia H. Aspöck & U. Aspöck, 1968

Ornatoraphidia H. Aspöck & U. Aspöck, 1968 (odescr) (described as a subgenus of *Raphidia* L.) [type species by original designation: *Raphidia etrusca* Albarda, 1891]: H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol, paras); Haring et al. 2011 (phyl); H. Aspöck 2012 (cat); U. Aspöck et al. 2012 (fig: phyltree); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy and systematics. H. Aspöck et al. (1991), Haring et al. (2011). *Ornatoraphidia* is markedly differentiated by morphological characters of adults and larvae. Based upon molecular phylogeny the sister taxon is *Turcoraphidia*. The genus comprises two species, which show very different patterns of distribution. Both species are known from Mediterranean islands.

Biology and ecology. Larvae living in upper layers of soil around roots of bushes. Development two years, see under *O. flavilabris*. Last hibernation stage: pupa or full-grown larva. Adults: IV–VI.

Distribution. Balkan Peninsula, Apennine Peninsula, southern parts of Central Europe.

Ornatoraphidia flavilabris (Costa, 1855)

Rhaphidia ophiopsis var. *flavilabris* Costa, 1855 (odescr): Pantaleoni 1999 (nom: earlier synonym of *Raphidia etrusca*), H. Aspöck and U. Aspöck 2013 (cat, etymol).

Raphidia etrusca Albarda, 1891 (odescr): H. Aspöck et al. 1991 (mon); Sziráki et al. 1992 (rec).

Ornatoraphidia etrusca (Albarda): Pantaleoni 1990a (com, rec); Pantaleoni 1990d [1993] (rec); H. Aspöck et al. 1991 (mon); Rausch and H. Aspöck 1991 (com, distr); Popov 1993 (rec); Letardi 1993 [1994] (rec); Pantaleoni et al. 1994 (distr, rec); U. Aspöck et al. 1995 (ethol: cop); H. Aspöck and Hölzel 1996 (distr); Letardi and Pantaleoni 1996 (rec); Popov 1997 (rec); Wachmann and Saure 1997 (charact, fig: imag); Popov 2000a (rec), 2000b (rec), 2001 (rec); Pantaleoni 2005 (nom).

Ornatoraphidia flavilabris (Costa): H. Aspöck et al. 1991 (mon); Sziráki 1999 (rec); H. Aspöck et al. 2001 (anncat); Letardi and Migliaccio 2002 (list); U. Aspöck and H. Aspöck 2005b (ill: ♂ gs); U. Aspöck and H. Aspöck 2005b (biogeogr); Pantaleoni 2005 (nom, rec); Anderle and U. Aspöck 2007 (rec); H. Aspöck and U. Aspöck 2007 (biogeogr, distr); Badano 2008 (distr, rec); H. Aspöck and U. Aspöck 2009 (ill: ♂ pu); Aistleitner and Gruppe 2009 (rec); Badano and Letardi 2010 (rec); Klokočovník et al. 2010 (rec); Letardi et al. 2010 (rec); Haring et al. 2011 (phyl, phyltree); H. Aspöck and U. Aspöck 2013 (cat, etymol; ill: imag, la, ♂ imag, pu); H. Aspöck and U. Aspöck 2014 (cat); Sziráki 2014 (rec); Letardi 2015 (rec); Tillier 2015 (rec); Devetak et al. 2015 (rec); Devetak and Rausch 2016 (rec); Hiemann et al. 2018 (rec); H. Aspöck et al. 2021 (phylogeogr); Tillier et al. 2022a (rec); Gruppe et al. 2023 (biol).

Raphidia luigionii Navás, 1927a (odescr): H. Aspöck et al. 1991 (mon); H. Aspöck and U. Aspöck 2014 (cat).

Raphidia regisborisi Navás, 1929 (odescr): H. Aspöck et al. 1991 (mon); H. Aspöck and U. Aspöck 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). *O. flavilabris* can easily be differentiated from the second species of the genus, *O. christianodagmara*, by morphological characters (brown pterostigma with yellowish zone along the costa) (Fig. 2g, h).

Biology and ecology. Larvae (Fig. 3a) soil-dwelling. Development variable: Pupation may take place already in the second year (i.e. after one hibernation of the larva) and the last hibernation stage may be the pupa or the prepupa. At least, under experimental conditions with more or less natural temperatures, sometimes full-grown larvae may pupate in winter, sometimes full-grown larvae overwinter and pupate in spring. At any rate, adults always appear in spring. In the field, imagines can be found – depending on the altitude – from IV to VI/VII. The species is thermophilic, but euryoecious and occurs in a great variety of habitats, preferably with light bush vegetation, particularly also in light forests of various kinds and also in macchia habitats in altitudes of 100 to 2200 m. *O. flavilabris* has repeatedly been found above the timberline.

Records on Mediterranean islands (Fig. 8b). *O. flavilabris* occurs on the island of Levkas (records at about 100 m asl); it will, however, probably be found also on other Ionian islands and possibly also on islands in the Adriatic Sea. Syntopic Raphidioptera on Levkas: *Parvoraphidia microstigma*, *Phaeostigma* (*Magnoraphidia*) *major*, *Subilla artemis*.

Continental distribution. The distribution of *O. flavilabris* comprises southern and northwestern parts of the Balkan Peninsula with a gap in large central parts, the whole Apennine Peninsula, eastern and southern parts of Austria, northwestern parts of Hungary, and the southeast of France.

Biogeography. *O. flavilabris* represents a polycentric Balkanopontomediterranean-Adriatomediterranean element with moderate expansivity. The populations of the southern Balkan Peninsula show considerable genetic (but not morphological) differences to populations from the Apennine Peninsula and from Central Europe.

***Ornatoraphidia christianodagmara* (H. Aspöck & U. Aspöck, 1970)**

Raphidia (*Ornatoraphidia*) *christianodagmara* H. Aspöck & U. Aspöck, 1970 (odescr, ecol); H. Aspöck et al. 1991 (mon).

Ornatoraphidia christianodagmara (H. Aspöck & U. Aspöck): H. Aspöck et al. 1991 (mon); Popov 1992 (biogeogr); Rausch and H. Aspöck 1992 (biol, distr, ecol, rec, tax, ill: la, map); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat); Sziráki 2014 (rec).

Taxonomy. H. Aspöck et al. (1991), Rausch and Aspöck (1992). The species can be easily differentiated from *O. flavilabris* eidonomically by the yellow pterostigma.

Biology and ecology. Larvae are soil-dwelling (although this needs confirmation). Development two years. Pupation in late autumn or even in winter, in one case pupation took place in March. Adults: V–VI. Findings of adults in light *Castanea sativa* forests (Euboea) and in light fir tree (*Abies cephalonica*) forests (Parnis mountains).

Records on Mediterranean islands (Fig. 9a). Euboea (Ochi mountains, 1100 m). Syntopic Raphidiop-tera species on Euboea: *Phaeostigma* (*Ph.*) *euboica*, *Phaeostigma* (*Magnoraphidia*) *wewalkai*, and *Raphidia* (*R.*) *mediterranea*.

Continental distribution. The species is only known from the Parnis Mts. in Attica, and in the Athmanon Mts. in Thessalia, Greece, where it occurs in altitudes of 850–1120 m.

Biogeography. Monocentric, stationary Balkanopontomediterranean faunal element.

***Phaeostigma* Navás, 1909, s.l.**

Phaeostigma Navás, 1909 (described as a section of *Raphidia* L.) [type species by subsequent designation: *Raphidia notata* Fabricius, 1781]: U. Aspöck and H. Aspöck 1989 (syst); U. Aspöck and H. Aspöck 1990 (syst); H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); Wachmann and Saure 1997 (charact); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol, paras); U. Aspöck 2002 (compmorph); H. Aspöck and U. Aspöck 2007 (ill: map); Monserrat and Papenberg 2010 (bibliogr, biogeogr, biol, chorol, descr, distr, synlist, tax); Haring et al. 2011 (fig:distrmap; phyl, phyltree); U. Aspöck et al. 2012 (fig: phyltree; list); H. Aspöck and U. Aspöck 2013 (cat, etymol, phyl), 2014 (cat); Monserrat and Papenberg 2015 (mon).

Taxonomy and systematics. H. Aspöck et al. (1991), Haring et al. (2011). With 41 species and three additional subspecies, *Phaeostigma* is (after *Mongoloraphidia*) the second largest genus of the family (and of the order). It comprises nine subgenera, seven of these with altogether 12 species are also represented on Mediterranean islands. *Phaeostigma* is morphologically clearly differentiated. Based on molecular phylogeny it is the sister group of the

rest of the *Phaeostigma* clade, i.e. (*Subilla* + *Ulrike*) + [(*Tjederiraphidia* + *Dichostigma*) + *Raphidia*] (Haring et al. 2011). The phylogeny of the subgenera of *Phaeostigma* has not yet been studied; so far only considerations based upon morphological criteria are available (H. Aspöck et al. 1991).

Biology. Larvae of many species corticolous, of many other species soil-dwelling. Development usually two or three years. Last hibernation stage: full-grown larva. Adults: IV–VII(VIII).

Distribution. The distribution of *Phaeostigma* s.l. comprises Europe (except the northernmost parts of the continent, the largest part of the Iberian Peninsula, Sicily, Sardinia, Corsica and several islands in the Aegean Sea) as far as to the Ural, Anatolia, the Caucasus region, Lebanon, Syria, northern Iraq, northern Iran. Several Mediterranean islands harbor at least one species: Levkas, Kefalonia, Thasos, Skopelos, Euboea, Crete, Karpathos, Ikaria, Samos, Lesbos, Chios, Rhodes, Cyprus.

Subgenus *Phaeostigma* Navás, 1909, s.str.

Phaeostigma Navás, 1909 (described as a section of *Raphidia* L.) [type species by subsequent designation: *Raphidia notata* Fabricius, 1781]: H. Aspöck et al. 1991 (mon); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol); U. Aspöck 2002 (compmorph); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat); Monserrat and Papenberg 2015 (synlist).

Erma Navás, 1918a (odescr) [type species by subsequent designation and monotypy: *Erma abdita* Navás, 1918a]: H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck and U. Aspöck 2014 (cat).

Navasana Steinmann, 1963 (odescr) [type species by original designation: *Navasana perumbrata* Steinmann, 1963]: H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck and U. Aspöck 2014 (cat).

Note. The subgenus *Phaeostigma* comprises six known species, one of these occurs on the island of Euboea.

***Phaeostigma* (*Phaeostigma*) *euboica* (H. Aspöck & U. Aspöck, 1976)**

Raphidia (*Phaeostigma*) *euboica* H. Aspöck & U. Aspöck, 1976 (odescr): H. Aspöck et al. 1991 (mon).

Phaeostigma (*Phaeostigma*) *euboica* (H. Aspöck & U. Aspöck, 1976): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Popov 1992 (biogeogr); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). The species belongs to the *Ph. notata* complex; it can easily be identified by the characters of the genital segments.

Biology and ecology. Larvae most probably exclusively corticolous, preferably on conifers (*Abies*, *Pinus*).

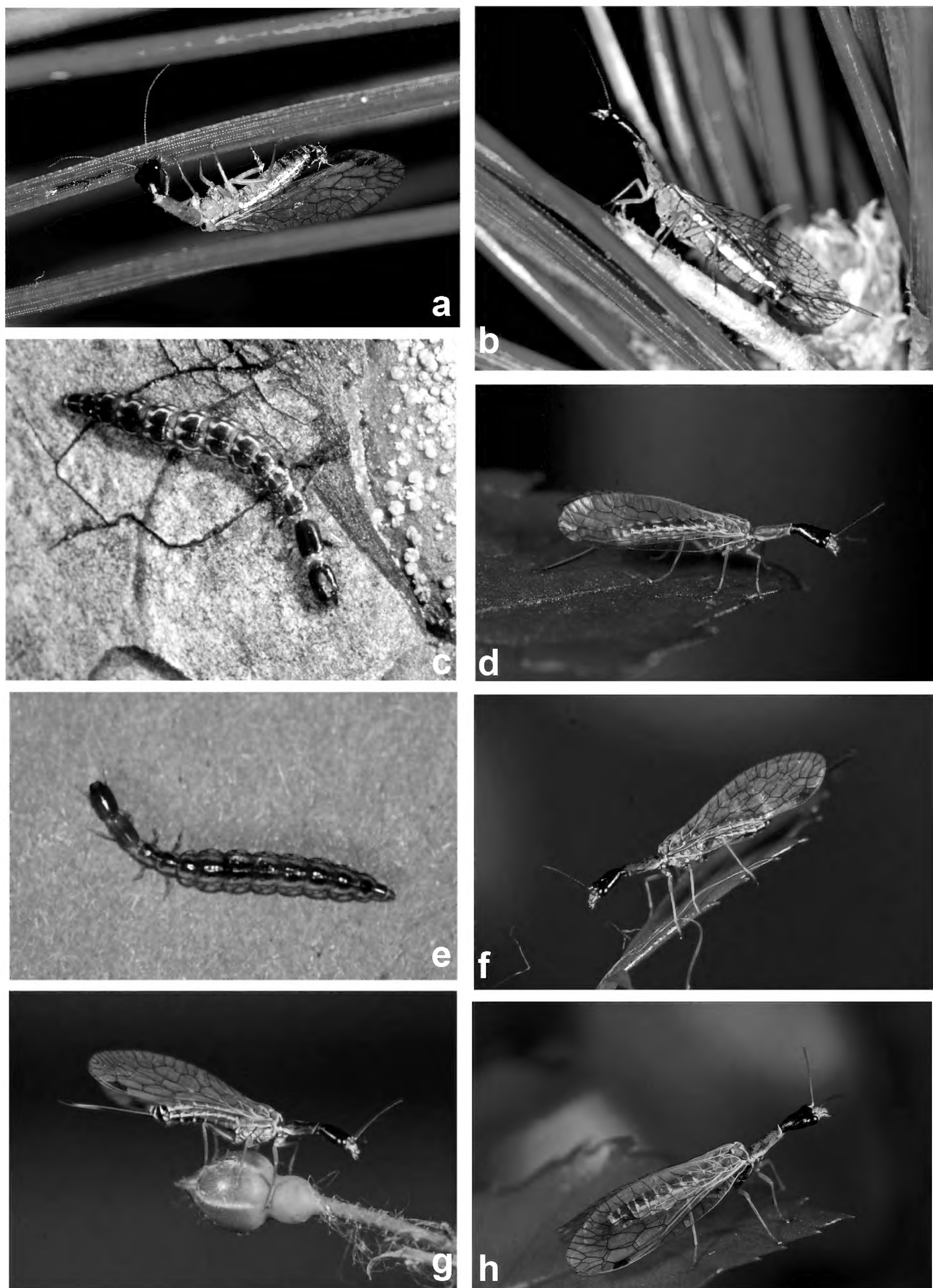


Figure 2. **a.** *Venustoraphidia nigricollis*, ♂. Lower Austria, Eichkogel near Mödling. Foto: H. Bruckner; **b.** *Venustoraphidia nigricollis*, ♀. Austria, Vienna. Foto: H. Bruckner; **c.** *Venustoraphidia nigricollis*, larva. Austria, Vienna. Foto: H. Bruckner; **d.** *Xanthostigma corsica*, ♀. Italy, Calabria, Aspromonte, Montalto. Foto: P. Sehnal; **e.** *Xanthostigma corsica*, larva. Italy, Calabria, Aspromonte, Montalto. Foto: F. Anderle, now Denner; **f.** *Parvoraphidia microstigma*, ♀. Greece, Phokis, Lidorikion mts. Foto: P. Sehnal; **g.** *Ornatoraphidia flavilabris*, ♀. Greece, Phokis, Lidorikion mts. Foto: P. Sehnal; **h.** *Ornatoraphidia flavilabris*, ♂. Greece, Viotia, Parnassos. Foto: P. Sehnal.

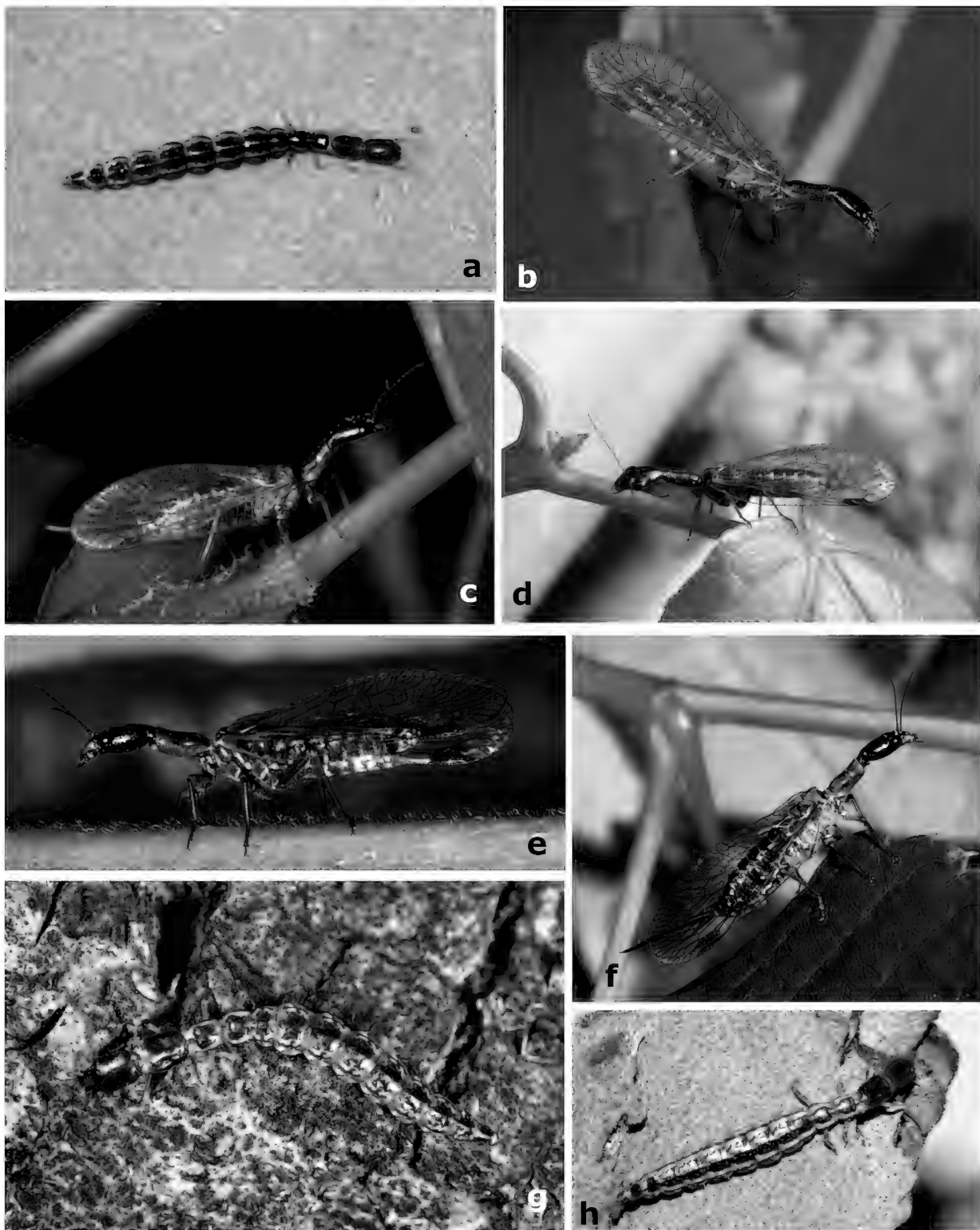


Figure 3. **a.** *Ornatoraphidia flavilabris*, larva. Italy, Calabria, Sila Grande. Foto: F. Anderle, now Denner; **b.** *Phaeostigma* (*Graecoraphidia*) *d. divina*, ♂. Greece, Viotia, Parnassos. Foto: P. Sehnal; **c.** *Phaeostigma* (*Graecoraphidia*) *d. divina*, ♀. Greece, Viotia, Parnassos. Foto: P. Sehnal; **d.** *Phaeostigma* (*Crassoraphidia*) *cyprica*, ♂. Cyprus, Troodos Mountain. Foto: H. Aspöck; **e.** *Phaeostigma* (*Magnoraphidia*) *major*, ♂. Lower Austria, Dürnstein. Foto: H. Bruckner; **f.** *Phaeostigma* (*Magnoraphidia*) *major*, ♀. Lower Austria, Dürnstein. Foto: H. Bruckner; **g.** *Phaeostigma* (*Magnoraphidia*) *major*, larva. Lower Austria, Eichkogel near Mödling. Foto: H. Bruckner; **h.** *Phaeostigma* (*Magnoraphidia*) *flammi*, larva. Greece, Pilon. Foto: H. Bruckner.

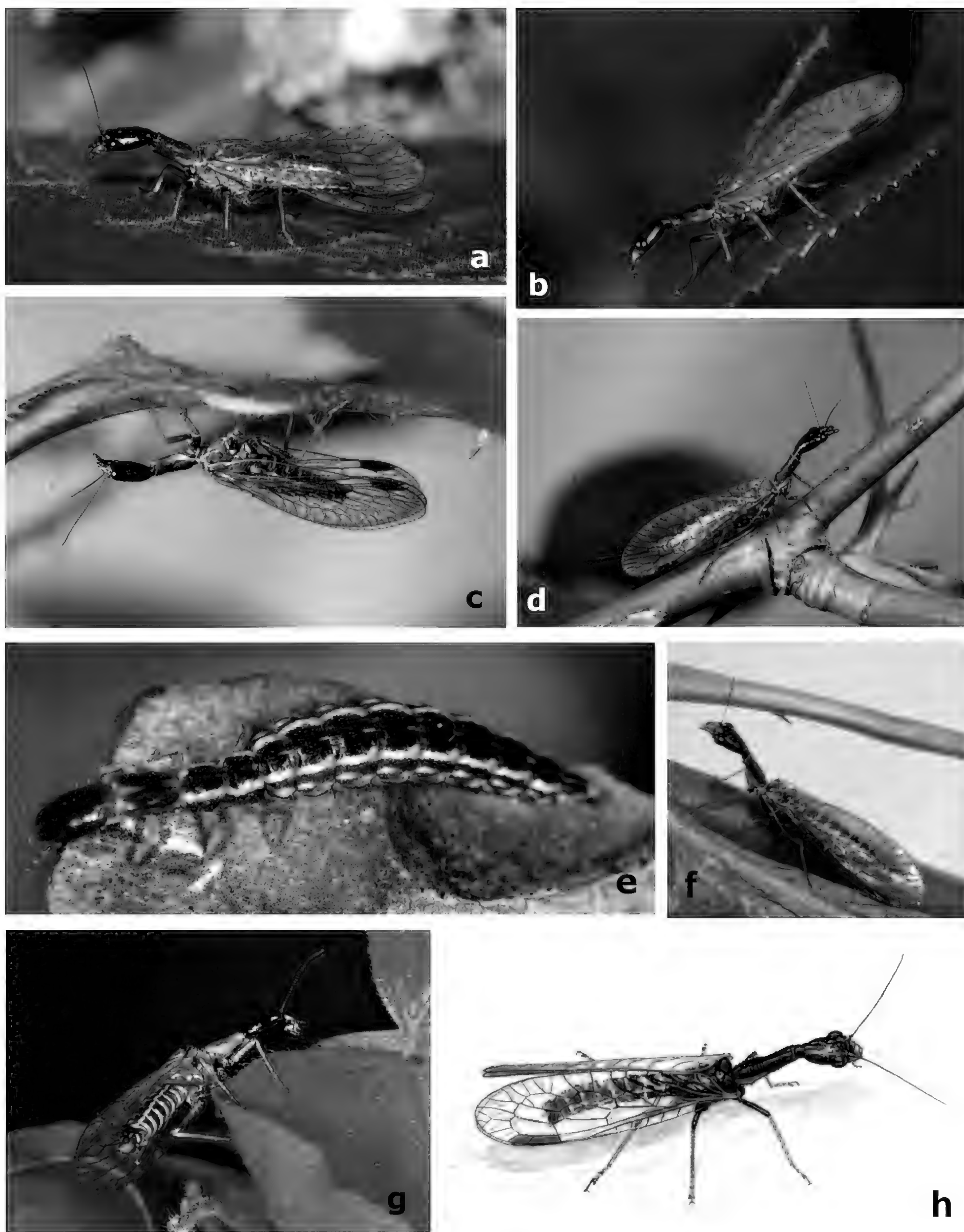


Figure 4. **a.** *Phaeostigma (Magnoraphidia) wewalkai*, ♂. Greece, Korinthia, Oros Onia. Foto: F. Anderle, now Denner; **b.** *Phaeostigma (Magnoraphidia) wewalkai*, ♀. Greece, Korinthia, Oros Onia. Foto: P. Sehnal; **c.** *Phaeostigma (Aegeoraphidia) biroi*, ♂. Greece, Crete, Anogia > Axos. Foto: P. Sehnal; **d.** *Phaeostigma (Aegeoraphidia) biroi*, ♀. Greece, Crete, Anogia > Axos. Foto: P. Sehnal; **e.** *Phaeostigma (Aegeoraphidia) biroi*, larva. Greece, Crete, Anogia > Axos. Foto: H. Bruckner; **f.** *Phaeostigma (Superboraphidia) minois*, ♂. Greece, Crete, Levka Ori, W Omalos. Foto: H. Aspöck; **g.** *Subilla confinis*, ♂. Lower Austria, Klosterneuburg. Foto: H. Bruckner; **h.** *Subilla principiae*, ♂. Italy, Sardinia, Gennargentu, Fonni. Watercolour by Wilhelm Zelenka (1936–2011), Vienna. In the possession of H. & U. Aspöck.

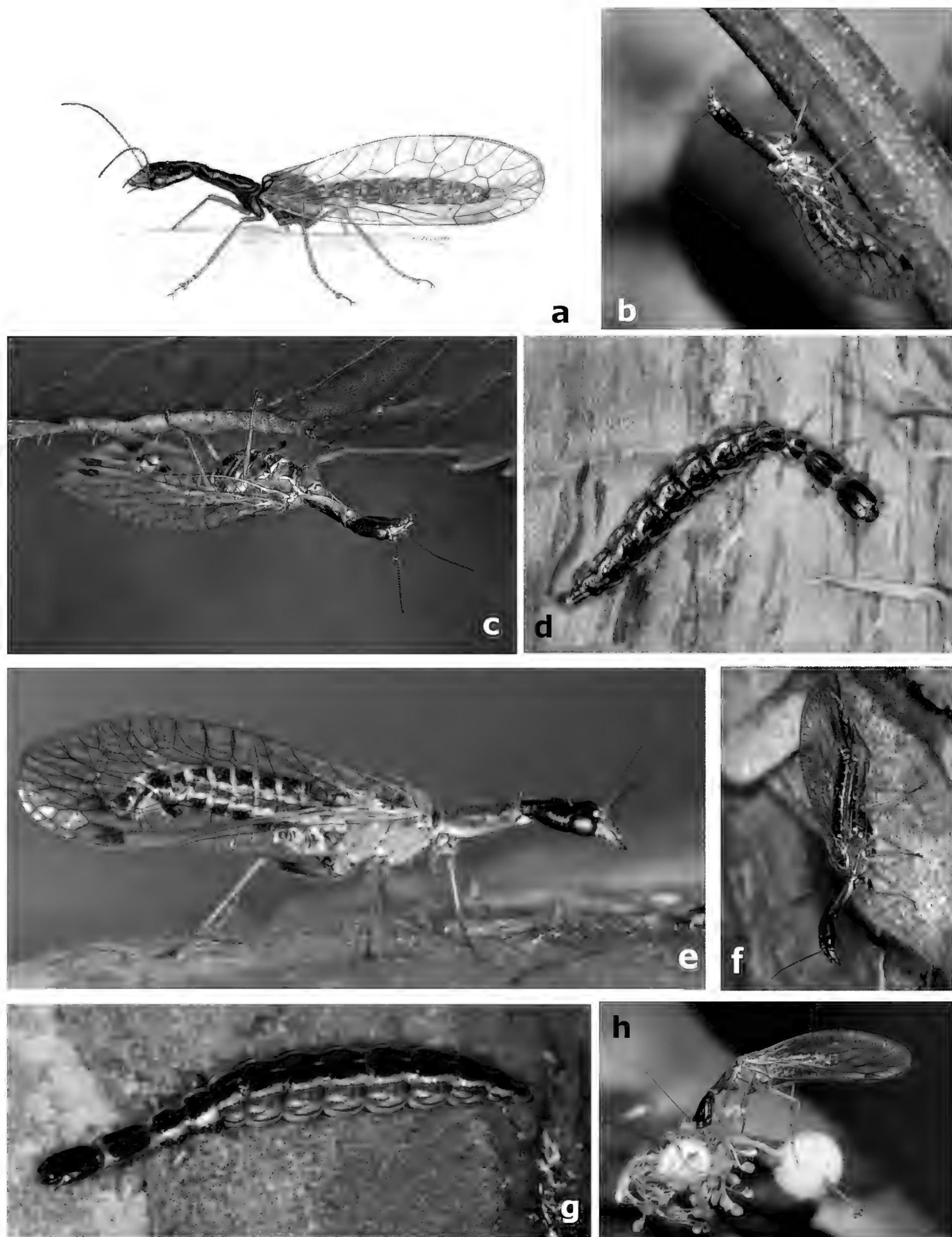


Figure 5. **a.** *Ulrike syriaca*, ♂. Cyprus, Limassol Forest. Watercolour by Wilhelm Zelenka (1936–2011), Vienna. In the possession of H. & U. Aspöck; **b.** *Raphidia mediterranea*, ♂. Upper Austria, Pelmburg near Helmonnsödt. Foto: H. Bruckner; **c.** *Raphidia mediterranea*, ♀. Upper Austria, Pelmburg near Helmonnsödt. Foto: H. Bruckner; **d.** *Raphidia mediterranea*, larva. Upper Austria, Pelmburg near Helmonnsödt. Foto: H. Bruckner; **e.** *Raphidia ariadne*, ♂. Greece, Crete, near Males. Foto: H. Bruckner; **f.** *Raphidia ariadne*, ♀. Greece, Crete, Anogia. Foto: H. Bruckner; **g.** *Raphidia ariadne*, larva. Greece, Crete, near Males. Foto: H. Bruckner; **h.** *Dichrostigma flavipes*, ♂. Lower Austria, Eichkogel near Mödling. Foto: F. Anderle, now Denner.

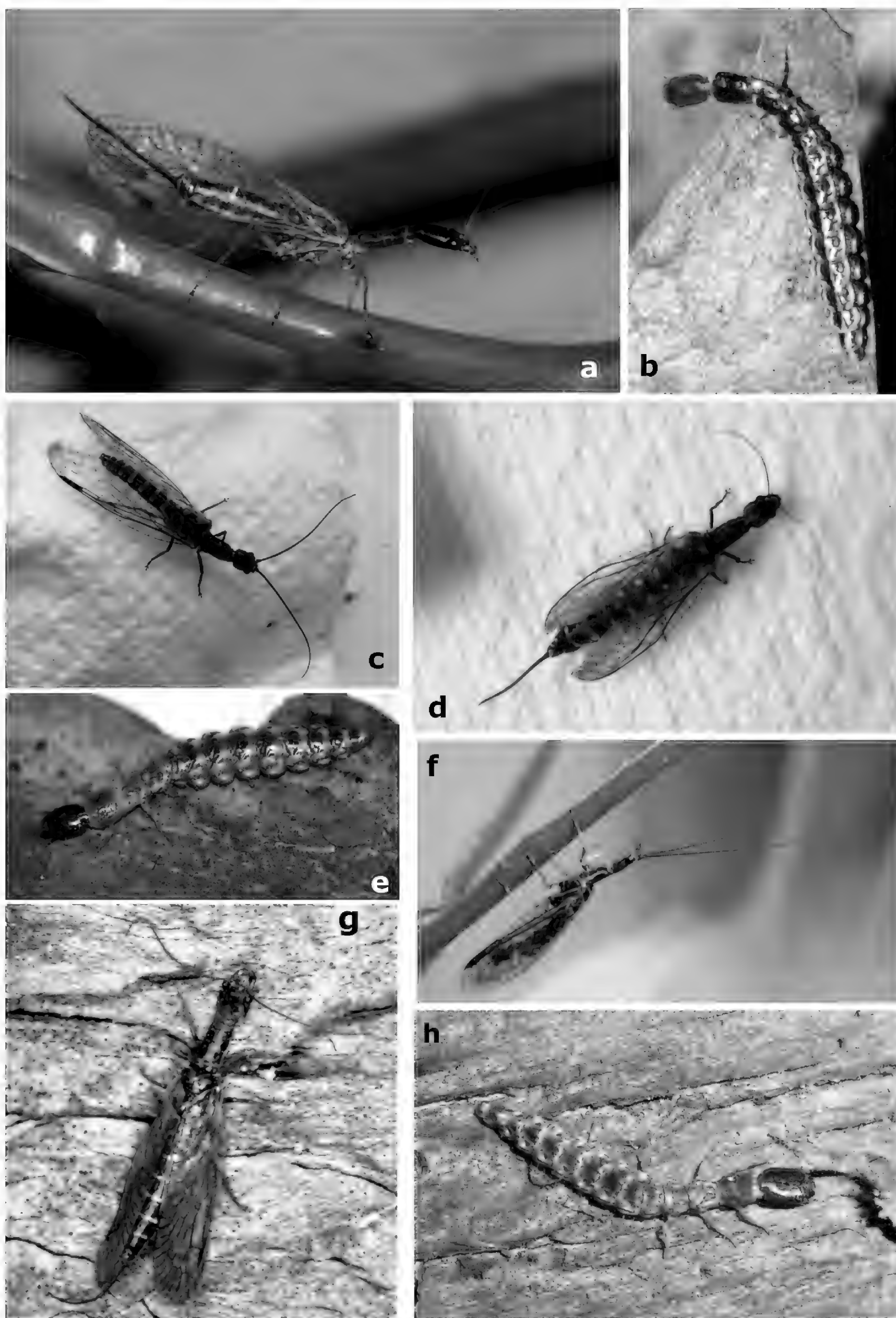


Figure 6. **a.** *Dichrostigma flavipes*, ♀. Lower Austria, Dürnstein. Foto: F. Anderle, now Denner; **b.** *Dichrostigma flavipes*, larva. Greece, Olympos. Foto: H. Bruckner; **c.** *Fibla (F.) maclachlani*, ♂. Italy, Sardinia, Supramonte. Foto: H. Aspöck; **d.** *Fibla (F.) maclachlani*, ♀. Italy, Sardinia, Gennargentu. Foto: H. Aspöck; **e.** *Fibla (F.) maclachlani*, larva. Italy, Sardinia, Gennargentu. Foto: F. Anderle, now Denner; **f.** *Fibla (Reisserella) pasiphae*, ♂. Greece, Crete, Levka Ori, W Omalos. Foto: H. Aspöck; **g.** *Fibla (Reisserella) pasiphae*, ♀. Crete, Tripti Forest. Foto: H. Paulus; **h.** *Fibla (Reisserella) pasiphae*, larva. Greece, Crete, Anogia > Axos. Foto: F. Anderle, now Denner.

Development two to three years. Last hibernation stage: full-grown larva. Adults: V–VI in light coniferous forests.

Records on Mediterranean islands (Fig. 7b). Central and southern parts of Euboea in altitudes of 700–1100 m only. Syntopic Raphidioptera: *Ornatoraphidia christianodagmara*, *Phaeostigma (Graecoraphidia) divina retsinata*, *Ph. (Magnoraphidia) flammi*, *Ph. (M.) wewalkai*, *Raphidia (R.) mediterranea*.

Biogeography. *Ph. euboica* is probably an endemism of Euboea. It represents a monocentric, extremely stationary Balkanopontomediterranean faunal element.

Subgenus *Graecoraphidia* H. Aspöck & U. Aspöck, 1968

Graecoraphidia H. Aspöck & U. Aspöck, 1968 (odescr) (described as a subgenus of *Raphidia* L.) [type species by original designation: *Raphidia divina* H. Aspöck & U. Aspöck, 1964a]: H. Aspöck et al. 1989 (biogeogr, distr; ill: distrmap); H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). *Graecoraphidia* is a well differentiated subgenus with three species, of which one – *Ph. (G.) divina* – comprises three subspecies, one of which occurs on Euboea (Fig. 3b).

Biology. Larvae (of all species and subspecies?) (Fig. 3c) living in the soil, but can also be corticolous. Development two to three years. Last hibernating stage: full-grown larva. Adults: (IV)V–VI(VII) in various habitats with deciduous trees and/or conifers in altitudes of 500–1200 m.

Distribution. The distribution of *Graecoraphidia* is restricted to a small part of southern Greece.

Phaeostigma (Graecoraphidia) divina H. Aspöck & U. Aspöck, 1964a

Raphidia divina H. Aspöck & U. Aspöck, 1964a (odescr): H. Aspöck et al. 1991 (mon); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2014 (cat).

Phaeostigma (Graecoraphidia) divina (H. Aspöck & U. Aspöck): H. Aspöck et al. 1991 (mon); Rausch and Aspöck 1991 (map); Popov 1992 (biogeogr); H. Aspöck et al. 2001 (anncat); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Note. Within this species three subspecies are differentiated, which occur in perfect geographic vicariance in small parts of southern Greece. One of these occurs on the island of Euboea.

Phaeostigma (Graecoraphidia) divina retsinata (H. Aspöck & U. Aspöck, 1973)

Raphidia (Graecoraphidia) divina retsinata H. Aspöck & U. Aspöck, 1973 (odescr): H. Aspöck et al. 1991 (mon).

Phaeostigma (Graecoraphidia) divina retsinata (H. Aspöck & U. Aspöck): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Rausch and H. Aspöck 1991 (ill: distrmap); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). *Ph. (G.) divina retsinata* can be differentiated from the other two subspecies by characters of the male genitalia, but also by eidonomic characters, such as the small size. The complicated taxonomic and systematic situation of the subspecies of *Ph. (G.) divina* needs an extensive phylogenomic study.

Biology and ecology. Larvae most probably soil-dwelling. Development under experimental conditions three years. Last hibernating stage: full-grown larva. Adults: V–VI. Most specimens were collected from fir trees in altitudes of 850–1100 m.

Records on Mediterranean islands (Fig. 9b). The subspecies was repeatedly found in a small area in Central Euboea. Syntopic Raphidioptera on Euboea: *Phaeostigma (Ph.) euboica*, *Ph. (Magnoraphidia) flammi*, *Ph. (M.) wewalkai*, *Raphidia (R.) mediterranea*.

Continental distribution. Greece (Parnis, Paterras mountains).

Biogeography. *Ph. (G.) divina retsinata* is an extremely stationary Balkanopontomediterranean faunal element with a few refugial subcenters within a small area in Greece.

Subgenus *Crassoraphidia* H. Aspöck & U. Aspöck, 1968

Crassoraphidia H. Aspöck & U. Aspöck, 1968 (odescr) (described as a subgenus of *Raphidia* L.) [type species by original designation: *Raphidia cyprica* Hagen, 1867]: H. Aspöck et al. 1989 (biogeogr, distr; ill: distrmap); H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). *Crassoraphidia* is a well differentiated subgenus with three species one of which occurring on the island of Cyprus.

Biology and ecology. Larvae are mainly soil-dwelling, but sometimes found under bark. Development two to three years. Last hibernation stage: full-grown larva. Adults: IV–VI(VII) in various kinds of light forests in altitudes of 600–1500 m.

Distribution. SW- and S-Anatolia, Cyprus, Lebanon.

Phaeostigma (Crassoraphidia) cyprica (Hagen, 1867)

Raphidia cyprica Hagen, 1867 (odescr): H. Aspöck et al. 1991 (mon). *Raphidia phoenicia* H. Aspöck & U. Aspöck, 1964a (odescr): H. Aspöck et al. 1991 (mon).

Phaeostigma (Crassoraphidia) cyprica (Hagen): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); H. Aspöck and Hölzel

1996 (distr); H. Aspöck et al. 2001 (anncat); Dobosz 2007 (distr, rec; ill: map); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat). *Phaeostigma cyprica* (Hagen): Haring et al. 2011 (phyl).

Taxonomy. *Crassoraphidia cyprica* (Fig. 3d) is closely related to *C. knappi*, from which it can be separated morphologically by slight differences of male and female genitalia.

Biology and ecology. Larvae were repeatedly found under the bark of pine trees. Development two to three years. Last hibernation stage: full-grown larva. Adults: IV–VI. Imagines were collected particularly on pine trees, in various light forests and forest-like habitats in altitudes from 1000–1850 m.

Records on Mediterranean islands (Fig. 10a). Cyprus. *Ph. (C.) cyprica* occurs in suitable habitats probably all over the island. Syntopic Raphidioptera in Cyprus: *Ulrike syriaca*.

Continental distribution. Lebanon.

Biogeography. Syrian (-Cyprian) faunal element. Most probably the refugial center was primarily somewhere in the Near East, from where the species invaded (passively) Cyprus. When and how this event may have happened, is unknown; it could have been during the last glacial period and/or possibly much later in the Holocene, perhaps even (repeatedly) by humans. Specimens from Cyprus cannot be differentiated morphologically from specimens from Near East. One may assume that genomic studies will lead to a better understanding.

Subgenus *Magnoraphidia* H. Aspöck & U. Aspöck, 1968

Magnoraphidia H. Aspöck & U. Aspöck, 1968 (odescr) (described as a subgenus of *Raphidia* L.) [type species by original designation: *Raphidia major* Burmeister, 1839]: H. Aspöck et al. 1989 (biogeogr, distr; ill: distrmap); H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Note. *Magnoraphidia* is – at least on the basis of characters of the male genitalia – a well differentiated subgenus with six known species. Three of these species have been found on Mediterranean islands.

Biology. Larvae of at least five species including those recorded from islands are corticolous. Development two, three or more years. Last hibernating stage: full-grown larva. Adults: (IV)V–VI(VII).

Distribution. Balkan Peninsula, Eastern Europe, Central Europe.

Phaeostigma (Magnoraphidia) major (Burmeister, 1839)

Raphidia major Burmeister, 1839 (odescr): H. Aspöck et al. 1991 (mon).

Phaeostigma (Magnoraphidia) major (Burmeister 1839): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Devetak 1992b (distr); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); Tröger 2002 (rec); U. Aspöck and H. Aspöck 2005a (biogeogr); U. Aspöck and H. Aspöck 2005b (ill: pu); Lange 2010 (rec); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat); Sziráki 2014 (rec); Weissmair et al. 2021 (biol, ecol).

Phaeostigma major (Burmeister): H. Aspöck et al. 1991 (mon); Saure and Gerstberger 1991 (ecol, rec); Horstmann 1994 (paras); Röhricht 1996 (rec); Saure 1996 (biogeogr, ecol, rec); Sziráki and Popov 1996 (rec); Achtelig 1997 (ecol, rec); Sziráki 1999 (rec); Röhricht 2000 (rec); Ábrahám 2001 (list, rec); Gruppe et al. 2004 (ecol, rec); Popov 2004 (chorol); Ábrahám 2006 (rec); Gruppe 2006b (ecol, rec); Gruppe and Müller 2007 (ecol, rec); Gruppe 2008 (ecol, rec).

Phaeostigma (Magnoraphidia) majus (Burmeister): Letardi et al. 2010 (rec).

Phaeostigma majus (Burmeister): Tillier et al. 2022a (rec).

Taxonomy. H. Aspöck et al. (1991). *Ph. (M.) major* (Fig. 3e, f) is the sister taxon of all other species of the major complex (i.e. all species of the subgenus except *Ph. (M.) klimeschi* (H. Aspöck & U. Aspöck) and can easily be distinguished in both sexes by characters of the genital segments.

Biology and ecology. Larvae (Fig. 3g) live under bark of a great variety of deciduous trees, but may sometimes (particularly in the southeast of Europe) be found on conifers. Development two, three or more years. Last hibernating stage: full-grown larva. Adults: (IV)V–VI(VII). *Ph. (M.) major* occurs in a great variety of habitats with trees in altitudes from 0 to ca. 1000 m.

Records on Mediterranean islands (Fig. 9a). Levkas, Kefalonia. Probably the species can also be found on other Ionian islands. Syntopic species on Levkas: *Parvorphidia microstigma*, *Ornatoraphidia flavilabris*, *Subilla artemis*, *Dichrostigma flavipes*.

Continental distribution. Balkan Peninsula, Central Europe (including eastern France and northern Germany), Eastern Europe.

Biogeography. *Ph. (M.) major* is a monocentric Balkanopontomediterranean faunal element with considerable expansivity. *Ph. major* is the only monocentric Balkanopontomediterranean snakefly which has reached the northern coast of Germany.

Phaeostigma (Magnoraphidia) flammi (H. Aspöck & U. Aspöck, 1973)

Raphidia (Magnoraphidia) flammi H. Aspöck & U. Aspöck, 1973 (odescr): H. Aspöck et al. 1991 (mon).

Phaeostigma (Magnoraphidia) flammi (H. Aspöck & U. Aspöck, 1973): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Popov 1992 (biogeogr); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). *Ph. (M.) flammi* (Fig. 3h) forms together with *Ph. (M.) horticola*, *Ph. (M.) robusta*, and *Ph. (M.) wewalkai* a group of closely related species within the *major* complex. These species can be differentiated only by characters of the genitalia, which is usually an easy task. However, on the island of Euboea where two of the three species – *Ph. (M.) flammi* and *Ph. (M.) wewalkai* – occur in a small area around the village of Seta in the Dirphys mountains intermediate individuals between *Ph. flammi* and *Ph. wewalkai* can be found, which we interpret as hybrids between the two species. On all other places on Euboea as well as on the continent the populations are homogenous.

Biology and ecology. Larvae (probably exclusively) corticolous on a great variety of deciduous trees and conifers in altitudes of 100 m (Skopelos) to 1100 m (Euboea). Development two to three (or more) years. Last hibernating stage: full-grown larva. Adults: V–VI.

Records on Mediterranean islands (Fig. 9a). Skopelos, Euboea.

Continental distribution. Confined to a small part of Greece (Stereia Ellas: Othrys, Pilion mountains).

Biogeography. Extremely stationary, monocentric Balkanopontomediterranean faunal element with several isolated populations confined to single mountain ranges.

***Phaeostigma (Magnoraphidia) wewalkai* (H. Aspöck & U. Aspöck, 1971)**

Raphidia (Magnoraphidia) wewalkai H. Aspöck & U. Aspöck, 1971a (odescr): H. Aspöck et al. 1991 (mon).

Phaeostigma (Magnoraphidia) wewalkai (H. Aspöck & U. Aspöck): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Popov 1992 (biogeogr); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol; ill: imag), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). *Ph. (M.) wewalkai* (Fig. 4a, b) can easily be distinguished from the species of its sister group (= (*Ph. flammi* + *Ph. horticola*) + *Ph. robusta*) by characters of the male and female genitalia. However, (at least) in a small area on the Dirphys mountain range on Euboea, where it occurs sympatric and syntopic with *Ph. (M.) flammi*, intermediate phaena occur. We interpret these phaena as hybrids between the two species. See also under *Ph. (M.) flammi*.

Biology and ecology. Larvae (probably exclusively) corticolous on deciduous trees and on conifers in various warmer habitats with rich vegetation from sea level to ca. 1000 m asl. Development two, three or more years. Last hibernation stage: full-grown larva. Adults: (IV)V–VI.

Records on Mediterranean islands (Fig. 8b). Euboea (Dirphys and Ochi mountain ranges) and various spots in the southwest of the island. Most probably the species occurs in all parts of Euboea.

Continental distribution. Restricted to a small part of eastern Sterea Ellas.

Biogeography. Extremely stationary, monocentric Balkanopontomediterranean faunal element.

Subgenus *Pontoraphidia* H. Aspöck & U. Aspöck, 1968

Pontoraphidia H. Aspöck & U. Aspöck, 1968 (odescr) (described as a subgenus of *Raphidia* L.) [type species by original designation: *Raphidia pontica* Albarda, 1891]: H. Aspöck et al. 1991 (mon); H. Aspöck et al. 1989 (biogeogr, distr; ill: distrmap); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol); H. Aspöck and U. Aspöck 2007 (ill: map); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Phidiara U. Aspöck & H. Aspöck, 1968 (odescr) (described as a subgenus of *Raphidia* L.) [type species by original designation: *Raphidia grandii* Principi, 1960]: H. Aspöck et al. 1991 (mon), H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). *Pontoraphidia* is a well differentiated subgenus with four species, one of them with two subspecies. The sister taxon is possibly *Magnoraphidia*.

Biology and ecology. Larvae of all species soil-dwelling in detritus between roots of bushes. Development two to three years. Adults: V–VIII, in various, particularly warmer habitats with rich vegetation of bushes in altitudes from 600–2200 m.

Distribution. The distribution comprises the southern parts of the Apennine Peninsula, the northern Balkan Peninsula, Eastern Europe and Anatolia.

***Phaeostigma (Pontoraphidia) setulosa* H. Aspöck & U. Aspöck, 1967b**

Raphidia setulosa H. Aspöck & U. Aspöck, 1967b (odescr): H. Aspöck et al. 1991 (mon).

Phaeostigma (Pontoraphidia) setulosa (H. Aspöck & U. Aspöck): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Canbulat and Kiyak 2006 (distr, rec; ill: map); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Phaeostigma setulosa (H. Aspöck & U. Aspöck): H. Aspöck et al. 1991 (mon); Sziráki and Popov 1996 (com, rec).

Taxonomy. H. Aspöck et al. (1991). *Ph. (P.) setulosa* is a polytypic species with scattered records within a considerably large distribution area: eastern Bulgaria (type locality), two spots in western Anatolia, Athos mountain, the island of Thasos, and northern Hungary. The populations from Thasos and Athos show differences compared to the other populations so that it seems justified to separate them at the level of subspecies. For a clarification of the somewhat complicated taxonomic situation within the species molecular phylogeny studies will be necessary. The sister species of *Ph. (P.) setulosa* is probably *Ph. (P.) pontica*.

***Phaeostigma (Pontoraphidia) setulosa aegea*
H. Aspöck, U. Aspöck & Rausch, 1991**

Phaeostigma (Pontoraphidia) setulosa aegea H. Aspöck, U. Aspöck & Rausch, 1991 (odescr, mon); H. Aspöck and Hölzel 1996 (distr); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). Eidonomic characters with those of *Ph. (P.) s. setulosa* agreeing, male and female genitalia, however, different.

Biology and ecology. Larvae most probably exclusively soil-dwelling. Development probably two to three years. Last hibernating stage: probably full-grown larva. Adults: (V)–VI. *Ph. (P.) s. aegea* was collected on the island of Thasos in glades within light pine forests at an altitude of about 1000 m in large numbers on fruits of *Asphodelus* (on the Athos Mountain in 1600 m on pine trees).

Records on Mediterranean islands (Fig. 9a). Thasos (Ipsarion). Syntopic Raphidioptera on Thasos: *Venustoraphidia nigricollis*, *Raphidia (R.) beieri*.

Continental distribution. Athos mountain (Chalkidiki, Greece).

Biogeography. *Ph. (P.) setulosa aegea* is an extremely stationary monocentric Balkanopontomediterranean faunal element. The species – *Ph. (P.) setulosa* (s. l.) – is a polycentric Balkanapontomediterranean-Anatolopontomediterranean faunal element of moderate expansivity. It will certainly be found in many parts of the Balkan Peninsula and in Anatolia.

Subgenus *Aegeoraphidia* H. Aspöck, U. Aspöck & Rausch, 1991

Aegeoraphidia H. Aspöck & U. Aspöck & Rausch, 1991 (odescr, mon) [type species by original designation: *Raphidia (Phidiara) raddai* U. Aspöck & H. Aspöck, 1969]. H. Aspöck et al. 1991 (mon); H. Aspöck 2002 (biol); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). This subgenus comprises two groups of species – the *raddai-ressli* group with five species (*Ph. (Ae.) raddai*, *Ph. (Ae.) resslis*, *Ph. (Ae.) prophetica*, *Ph. (Ae.) birois*, and *Ph. (Ae.) vartianorum*) and the *noane* group with two species (*Ph. (Ae.) noane* and *Ph. (Ae.) remane*). Of these, four species occur on Mediterranean islands. *Aegeoraphidia* can be clearly differentiated from other subgenera particularly by characters of the male genitalia. The sister group of the subgenus is still unknown.

Biology and ecology. Larvae of all species principally soil-dwelling, but larvae of some species can also be found under bark of various trees. Development two or three years. Adults: IV–VI, in various habitats in altitudes of 0–2200 m.

Distribution. The distribution of *Aegeoraphidia* comprises Crete, several islands in the eastern Aegean Sea, western, southern, and southeastern Anatolia, and northern Iraq.

***Phaeostigma (Aegeoraphidia) raddai* (U. Aspöck & H. Aspöck, 1969)**

Raphidia (Phidiara) raddai U. Aspöck & H. Aspöck, 1969 (odescr): H. Aspöck et al. 1991 (mon).

Phaeostigma (Aegeoraphidia) raddai (U. Aspöck & H. Aspöck): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); Canbulat and Kiyak 2006 (distr, rec; ill: map); Dobosz 2007 (distr, rec); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). *Ph. (Ae.) raddai* can be easily differentiated from the other species of the subgenus even by eidonomic characters and particularly by its typical male genitalia.

Biology and ecology. Larvae corticolous as well as soil-dwelling. Findings of larvae under bark of *Pinus*, but also of *Pyrus* and *Mastix* as well as in the detritus between and around roots of *Genista* and *Arbutus*. Development two, three or more years. Last hibernating stage: full-grown larva. Adults: IV–VI occurring in various habitats from sea level to 800 m.

Records on Mediterranean islands (Fig. 9b). Lesbos, Chios, Samos, Ikaria. The species will also be found on other islands in the eastern Aegean Sea. Syntopic Raphidioptera species: *Raphidia (R.) mysia* (Lesbos), *R. ambigua* (Samos), *R. peteressli* (Chios), *R. mediterranea* (Ikaria), *Parainocellia resslis* (Samos).

Continental distribution. Southwestern Anatolia.

Biogeography. Monocentric, stationary Anatolopontomediterranean faunal element comprising a relatively small area east of the Rechinger line.

***Phaeostigma (Aegeoraphidia) prophetica* (H. Aspöck & U. Aspöck, 1964a)**

Raphidia prophetica H. Aspöck & U. Aspöck, 1964a (odescr): H. Aspöck et al. 1991 (mon).

Phaeostigma resslis prophetica (H. Aspöck & U. Aspöck): H. Aspöck et al. 1991 (mon).

Phaeostigma prophetica (H. Aspöck & U. Aspöck): H. Aspöck et al. 1991 (mon); U. Aspöck and H. Aspöck 1989 (tax).

Phaeostigma (Aegeoraphidia) prophetica (H. Aspöck & U. Aspöck): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). Closely related to *Ph. (Ae.) resslis*, from which it can be differentiated only by fine, but always recognizable differences in the male genitalia. The main reason for treating *Ph. (Ae.) prophetica* as a species and not a subspecies of *Ph. (Ae.) resslis* is the fact that not *Ph. (Ae.) resslis* but another species of this clade, *Ph. (Ae.) vartianorum*, occurs in those parts of Anatolia opposite to Rhodes.

Biology and ecology. Larvae mainly soil-dwelling, but also corticolous on various trees (*Pinus*, *Quercus*, *Amygdalus*). Development (at least) two years. Last stage of hibernation: full-grown larva. Adults: (IV)V–VI in various habitats, particularly light forests of *Pinus* and *Quercus*. Records from 350–750 m.

Records on Mediterranean islands (Fig. 9b). Rhodes, probably endemic to this island and apparently occurring all over Rhodes. Syntopic Raphidioptera species: *Subilla colossea*, *Raphidia* (*R.*) *ambigua*.

Biogeography. Monocentric, extremely stationary Anatolopontomediterranean faunal element. Endemic to Rhodes.

***Phaeostigma* (*Aegeoraphidia*) *karpathana* (U. Aspöck & H. Aspöck, 1989)**

Phaeostigma (*Aegeoraphidia*) *karpathana* U. Aspöck & H. Aspöck, 1989 (odescr); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. U. Aspöck and H. Aspöck (1989). In its eidonomic characters the species agrees with *Ph. (Ae.) ressl*i and *Ph. (Ae.) prophetica*, but it can easily be differentiated by characters of the male and female genitalia.

Biology and ecology. Larvae soil-dwelling, but exceptionally also corticolous (findings on *Pyrus* with lichens on the stem). Development two years. Last hibernating stage: full-grown larva. Adults: (IV) V (-VI) in various habitats like pine forests (*Pinus halepensis*), open slopes with *Genista* and *Crataegus* in altitudes from 50–750 m. Adults in extraordinarily high numbers on *Genista fassellata* and also on young pine trees.

Records on Mediterranean islands (Fig. 9b). Only from Karpathos. Probably endemic to the island. Syntopic Raphidioptera species: *Raphidia* (*R.*) *mediterranea*. It is possible that *Ph. (Ae.) karpathana* occurs also on the near island of Kasos, but certainly not on other islands.

Biogeography. Monocentric, extremely stationary species, endemic to Karpathos. The species can neither be classified as Anatolopontomediterranean nor as a Cretan faunal element. It is assumed that Karpathos has represented a refugial center of its own during the glacial periods.

***Phaeostigma* (*Aegeoraphidia*) *biroi* (Navás, 1915)**

Lesna biroi Navás, 1915a (odescr); H. Aspöck et al. 1991 (mon).

*Raphidia labyrinth*a H. Aspöck & U. Aspöck, 1964a (odescr); H. Aspöck et al. 1991 (mon).

Phaeostigma biroi (Navás): H. Aspöck et al. 1991 (mon); U. Aspöck and H. Aspöck 1989 (tax); U. Aspöck and H. Aspöck 1990 (distr); Ábrahám and Papp 1994 (com, FD!).

Phaeostigma (*Aegeoraphidia*) *biroi* (Navás): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Popov 1992 (bio-

geogr); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); Tröger 2005a (rec); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol; ill: ♂ imag, pu), 2014 (cat); Sziráki 2014 (rec).

Taxonomy. H. Aspöck et al. (1991). *Ph. (Ae.) biroi* (Fig. 4c, d) is probably the sister taxon of the other species of the *biroi-ressli* complex, from which it can be clearly separated by characters of the male genitalia. Moreover, in most cases even a differentiation on the basis of eidonomic characters is possible: The pterostigma of *Ph. (Ae.) biroi* is in its distal part paler than proximally, sometimes even yellow. Moreover, *Ph. (Ae.) biroi* is the only *Aegeoraphidia* species occurring in Crete.

Biology and ecology. Larvae (Fig. 4e) probably corticolous (records from *Pinus*, *Amygdalus*, *Quercus*) and soil-dwelling. Development two or three years. Last hibernating stage: full-grown larva. Adults: IV–VI. Many records on *Genista*, *Ilex*, *Acer*, *Crataegus*, *Pinus brutia* in various, mainly warm and relatively dry habitats from sea level to 1500 m.

Records on Mediterranean islands (Fig. 9b). There are many records from Crete, but none from other islands. Syntopic Raphidioptera: *Phaeostigma* (*Superboraphidia*) *minois*, *Raphidia* (*R.*) *ariadne*, *Fibla* (*Reisserella*) *pasiphae*.

Biogeography. Monocentric, stationary Cretan faunal element. Endemic to Crete.

Subgenus *Superboraphidia* H. Aspöck & U. Aspöck, 1968

Superboraphidia H. Aspöck & U. Aspöck, 1968 (odescr) (described as a subgenus of *Raphidia* L.) [type species by original designation: *Raphidia auberti* H. Aspöck & U. Aspöck, 1966]: H. Aspöck et al. 1989 (biogeogr, distr; ill: distrmap); U. Aspöck and H. Aspöck 1990 (syst); H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

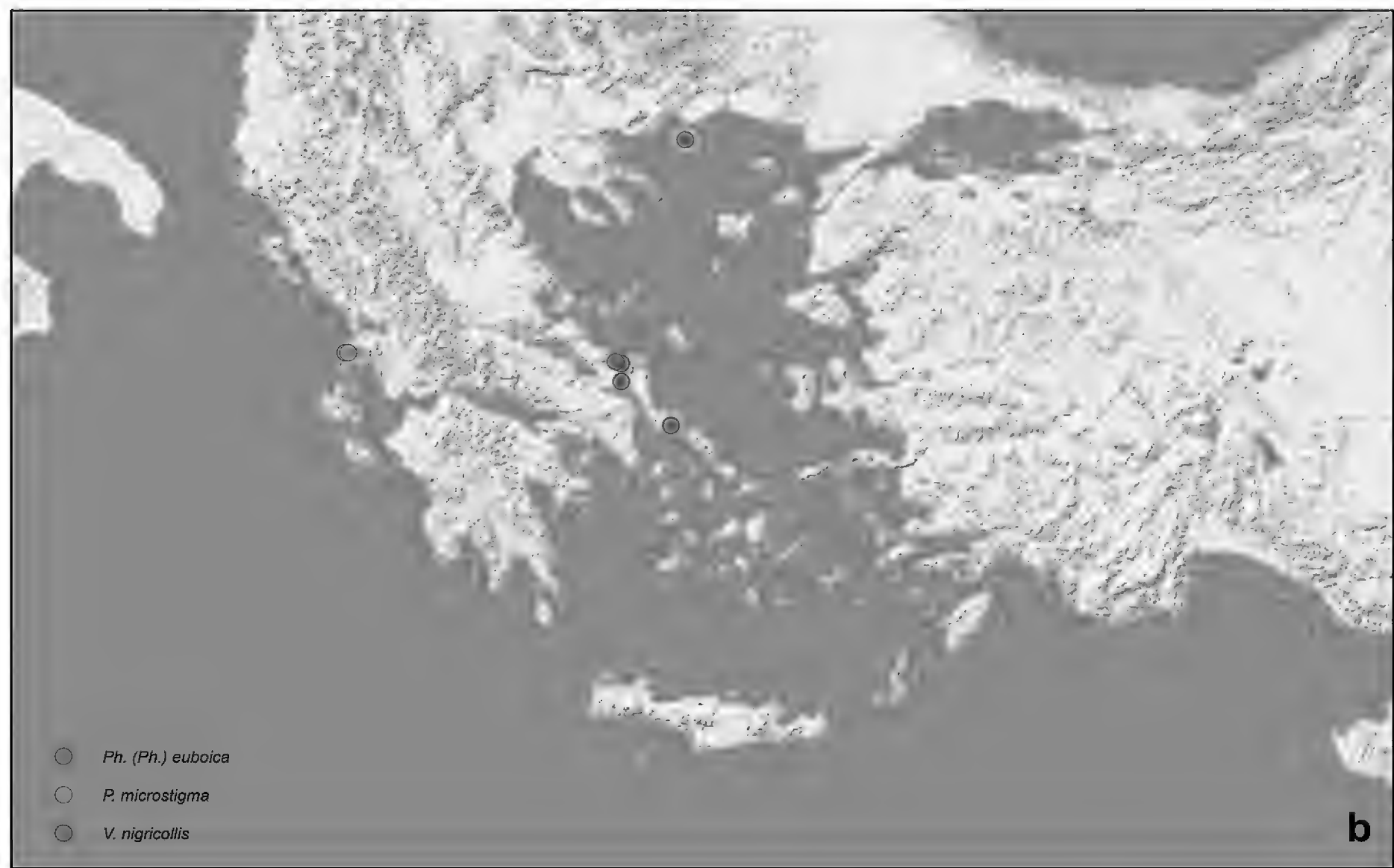
Taxonomy. H. Aspöck et al. (1991). *Superboraphidia* comprises five species (*Phaeostigma* (*S.*) *auberti*, *Ph. (S.) rauschi*, *Ph. (S.) mammaphila*, *Ph. (S.) turcica*, and *Ph. (S.) minois*), which are not closely related but show a special synapomorphy in the male genitalia, which justifies to unite them in a subgenus. One of the five species occurs on a Mediterranean island.

Biology. Larvae of probably all five species are soil-dwelling. Development insufficiently known, probably two years or longer. Last hibernating stage: full-grown larva. Adults: V–VII in various habitats, usually with rich low vegetation in higher elevations (800–1200 m), sometimes even above timberline.

Distribution. The distribution of *Superboraphidia* comprises southern parts of the mainland of Greece, the Peloponnisos and the west of Anatolia (H. Aspöck et al. 1991; Rausch and H. Aspöck 1992).



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Source: US National Park Service

Figure 7. a. Records of species of the family Raphidiidae, altogether 30 species on islands of the Mediterranean Sea; **b.** Records of *Venustoraphidia nigracollis*, *Phaeostigma (Ph.) euboica*, and of *Parvoraphidia microstigma*, on Mediterranean islands.



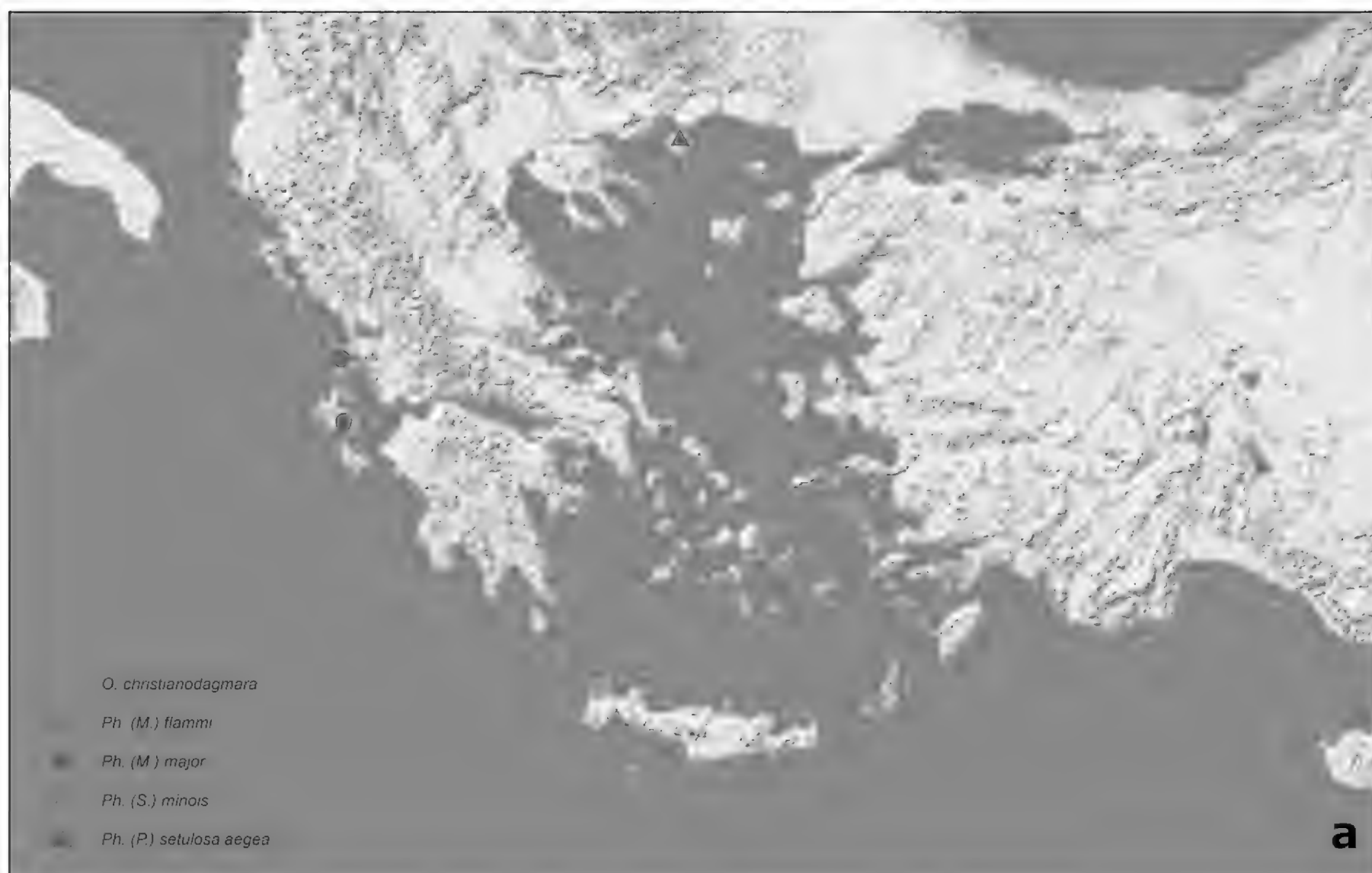
Figure 8. a. Records of species of the genus *Xanthostigma*, *X. corsica* and *X. aloysiana*, on Mediterranean islands; **b.** Records of *Ornatoraphidia flavilabris*, *Phaeostigma (Magnoraphidia) wewalkai*, and of *Dichrostigma flavipes*, on Mediterranean islands.

***Phaeostigma (Superboraphidia) minois* U. Aspöck & H. Aspöck, 1990**

Phaeostigma (Superboraphidia) minois U. Aspöck & H. Aspöck, 1990 (odescr, ecol, distr; ill: ♀ gs, ♂ gs, wings); Popov 1992 (biogeogr); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat);

Tröger 2005a (rec); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. U. Aspöck and H. Aspöck (1990). The species (Fig. 4f) is eidonomically similar to *Ph. (Aegeoraphidia) biroi*, but can be easily differentiated in both



Source: US National Park Service



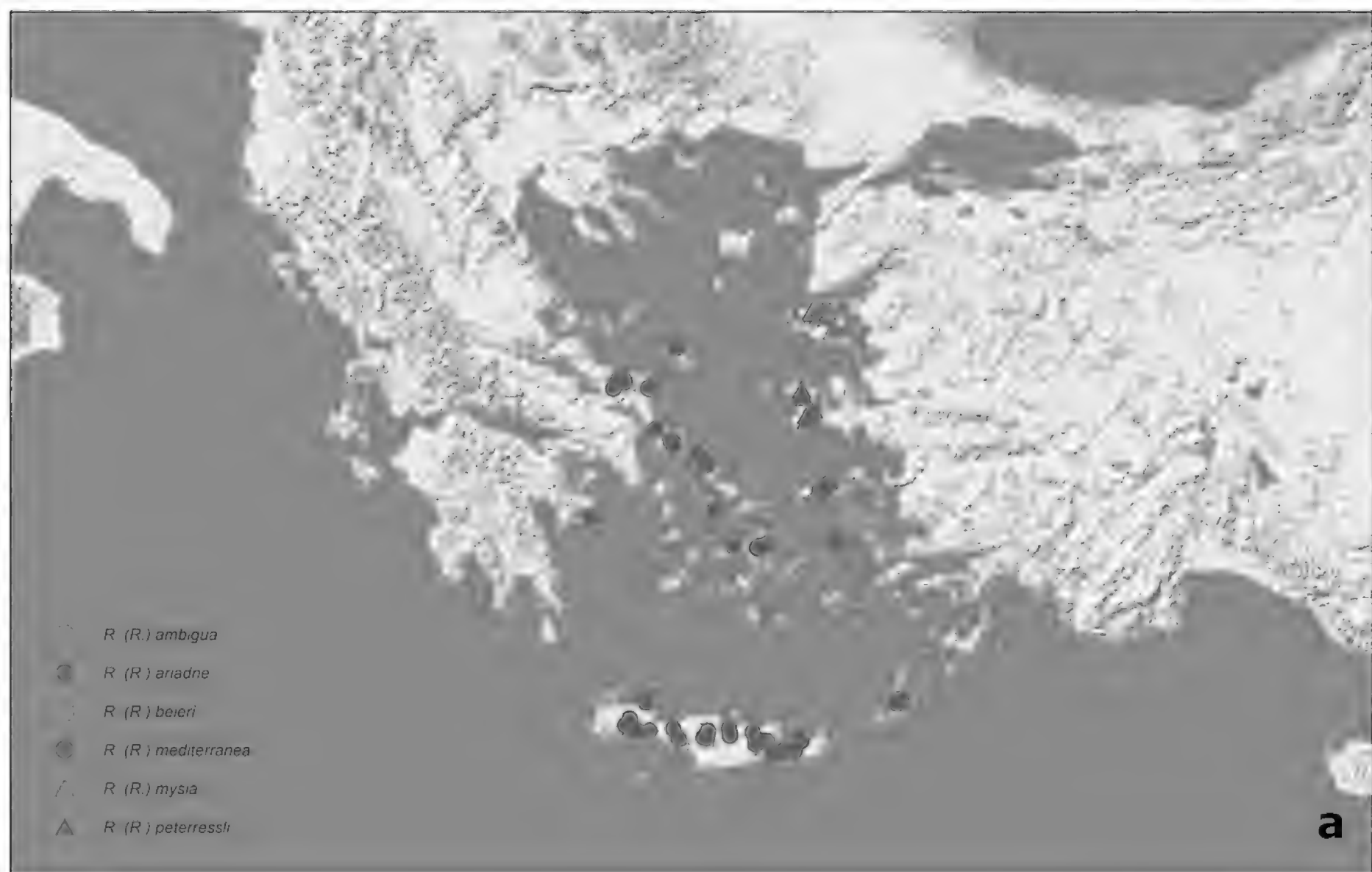
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Figure 9. a. Records of *Ornatoraphidia christianodagmara*, *Phaeostigma (Magnoraphidia) major*, *Ph. (M.) flammi*, *Ph. (Pontoraphidia) setulosa aegea*, and of *Ph. (Superboraphidia) minois*, on Mediterranean islands; **b.** Records of *Phaeostigma (Grecoraphidia) divina retsinata*, and of species of *Aegeoraphidia*, *Ph. (Aegeoraphidia) raddai*, *Ph. (Ae.) prophetica*, *Ph. (Ae.) karpathana*, and of *Ph. (Ae.) biroï*, on Mediterranean islands.



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Figure 10. a. Records of *Phaeostigma (Crassoraphidia) cyprica*, and of *Ulrike syriaca*, on Mediterranean islands; **b.** Records of species of the genus *Subilla*, *S. confinis*, *S. artemis*, *S. principiae*, and *S. colossea*, on Mediterranean islands.



Source: US National Park Service



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Figure 11. a. Records of species of the genus *Raphidia*, *R. (R.) mediterranea*, *R. (R.) beieri*, *R. (R.) peterressli*, *R. (R.) mysia*, *R. (R.) ambigua*, and *R. (R.) ariadne*, on Mediterranean islands; **b.** Records of species of the family Inocelliidae, *Fibla (F.) maclachlani*, *Fibla (Reisserella) pasiphae*, and *Parainocellia ressl*, on Mediterranean islands.

sexes by characters of the genitalia. The sister taxon is unknown, and the species has a rather isolated position within the subgenus.

Biology and ecology. Larvae probably soil-dwelling. Larvae and development unknown. Adults: V, on *Pinus brutia* and *Cypressus sempervivens*, in light forests with *Quercus*, *Crataegus* etc. in 830–1100 m.

Records on Mediterranean islands (Fig. 9a). *Ph. (S.) minois* has so far only been found in a few spots near the Omalos Plateau in the west of Crete (Chania). Syntopic Raphidioptera: *Phaeostigma (Aegeoraphidia) biroi*, *Raphidia (R.) ariadne*, *Fibla (Reisserella) pasiphae*.

Biogeography. Endemic to Crete. Monocentric, (extremely) stationary Cretan faunal element.

Subilla Navás, 1916

Subilla Navás, 1916 (odescr) [type species by original designation: *Raphidia sericea* Albarda, 1891]: H. Aspöck et al. 1989 (biogeogr, distr; ill: distrmap); H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol, paras); H. Aspöck and U. Aspöck 2007 (ill: map); Monserrat and Papenberg 2010 (biogeogr, chorol); Haring et al. 2011 (phyl); U. Aspöck et al. 2012 (fig: phyltree; list); H. Aspöck and U. Aspöck 2013 (cat, etymol, phyl), 2014 (cat); Monserrat and Papenberg 2015 (synlist).

Taxonomy and systematics. H. Aspöck et al. (1991), Haring et al. (2011). *Subilla* is a very conspicuous genus clearly differentiated by imaginal as well as by larval characters from all other genera of the family. The sister taxon is probably *Tauroraphidia* H. Aspöck & U. Aspöck & Rausch, 1982. In the molecular phylogenetic analysis of the Raphidiidae (Haring et al. 2011) the genus *Ulrike* H. Aspöck emerged as the sister taxon of *Subilla*, however, *Tauroraphidia* was not available for this analysis. The genus comprises altogether ten species, five of these (*S. confinis*, *S. aliena*, *S. artemis*, *S. xylidiophila*, *S. walteri*) form the *confinis*-group, three others (*S. physodes*, *S. priapella*, *S. colossea*) the *physodes*-group, while *S. fatma* and *S. principiae* are somewhat isolated, although they show affinities to the *physodes*-group.

Biology and ecology. Larvae of all species corticolous, some species particularly on *Quercus*, some (also or preferably) on conifers (*Pinus*, *Abies*). Development at least two or three years. Last hibernating stage: full-grown larva. Adults: (IV)V–VI(VII).

Distribution. All European peninsulas, Central, Western and Eastern Europe, Anatolia. Altogether four species have been found on Mediterranean islands: Sardinia, Sicily, Levkas, Rhodes. Each of these islands harbors only one *Subilla* species.

Subilla confinis (Stephens, 1836)

Raphidia confinis Stephens, 1836 (odescr): H. Aspöck et al. 1991 (mon); Suntrup 1990 (ecol, paras, rec); Ábrahám 1992 (rec); Schmitz 1992 (ecol, rec).

Raphidia cognata Rambur, 1842 (odescr): H. Aspöck et al. 1991 (mon). *Raphidia schneideri* Ratzeburg, 1844 (odescr): H. Aspöck et al. 1991 (mon). *Raphidia colubroides* Costa, 1855 (odescr): H. Aspöck et al. 1991 (mon). *Raphidia sericea* Albarda, 1891 (odescr): H. Aspöck et al. 1991 (mon). *Subilla confinis* (Stephens): H. Aspöck et al. 1991 (mon); Kielhorn 1991 (ecol, rec); Saure and Gerstberger 1991 (ecol, rec); Ábrahám 1992 (rec); Plant 1992 (com, rec); Morgan 1993 (rec); Horstmann 1994 (paras); Plant 1994 (biol, distrmap, tax); H. Aspöck and Hölzel 1996 (distr); Röhricht 1996 (rec); Saure 1996 (biogeogr, ecol, rec); Achtelig 1997 (ecol, rec); Schubert and Gruppe 1999 (ecol, rec); Sziráki 1999 (rec); Röhricht 2000 (rec); Ábrahám 2001 (list, rec); H. Aspöck et al. 2001 (anncat); Gruppe and Schubert 2001 (ecol, rec); Plant 2001 (com, rec); Vas et al. 2001 (ecol, rec); Popov 2002 (biogeogr); Gruppe et al. 2004 (ecol, rec); Haring and U. Aspöck 2004 (phyl); Pantaleoni et al. 2005 (tax); Pantaleoni 2005 (rec); Ábrahám 2006 (rec); H. Aspöck and U. Aspöck 2007 (biogeogr, distr); Gruppe 2007a (rec); Gruppe and Müller 2007 (ecol, rec); Gruppe 2008 (ecol, rec); Weigelmeier 2008 (biol); Letardi et al. 2010 (rec); Nicoli Aldini et al. 2012 (rec, distr); Haring et al. 2011 (phyl, phyltree); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat); Morinière et al. 2014 (barcode, phyl); Gruppe 2015 (ecol, rec); Weissmair et al. 2021 (biol, ecol).

Taxonomy. H. Aspöck et al. (1991). *S. confinis* (Fig. 4g) is eidonomically very similar to the other four species of the *confinis*-group (*S. aliena*, *S. xylidiophila*, *S. artemis*, *S. walteri*), but can easily be differentiated by characters of the male genitalia. Moreover, no island harbors more than one species.

Biology and ecology. Larvae exclusively corticolous on *Quercus*, *Acer*, *Pinus*, *Malus*, very rarely (in the south of Italy) on *Pinus* in light forests and gardens, mostly from sea level to ca. 500 m, in the south of Italy up to 1400 m. Development usually two or three years. Last hibernating stage: full-grown larva. Adults: (IV) V–VI (VII).

Records on Mediterranean islands (Fig. 10b). There are only a few records in the northeast of Sicily. Syntopic other Raphidioptera in Sicily: *X. corsica*, *F. maclachlani*.

Continental distribution. Apennine Peninsula, Central Europe, France, England, Denmark, Eastern Europe.

Biogeography. Expansive probably monocentric Adriatomediterranean faunal element.

Subilla artemis (H. Aspöck & U. Aspöck, 1971)

Raphidia (Subilla) artemis H. Aspöck & U. Aspöck, 1971 (odescr): H. Aspöck et al. 1991 (mon).

Subilla artemis (H. Aspöck & U. Aspöck, 1971): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Popov 1992 (biogeogr); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); Pantaleoni et al. 2005 (tax); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). *S. artemis* belongs to the *confinis*-group of the genus and is eidonomically similar to the other species. Although the male genitalia show a surprising variability, they always allow to identify the species reliably.

Biology and ecology. Larvae corticolous on *Quercus*, *Amygdalus*, *Pyrus*, *Crataegus* and other deciduous trees, very rarely on *Pinus* in light forests in 100–1100 m. Development two to three years. Last hibernating stage: full-grown larva. Adults: V–VI.

Records on Mediterranean islands (Fig. 10b). Levkas. Syntopic Raphidioptera on Levkas: *Parvora-phidia microstigma*, *Ornatoraphidia flavilabris*, *Phaeostigma* (*Magnoraphidia*) *major*.

Continental distribution. Greece north of the Gulf of Korinthos, North Macedonia.

Biogeography. *S. artemis* is a monocentric Balkanopontomediterranean faunal element with moderate expansivity.

***Subilla principiae* Pantaleoni, U. Aspöck, Cao & H. Aspöck, 2005**

Subilla principiae Pantaleoni, U. Aspöck, Cao & H. Aspöck, 2005 (odescr); H. Aspöck and U. Aspöck 2007a (biogeogr, distr); U. Aspöck and H. Aspöck 2007 (ill: ♂ imag); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. Pantaleoni et al. (2005). *S. principiae* (Fig. 4h) can clearly be differentiated from all other species of the genus by characters of the male and female genitalia. Moreover, the species can be readily recognized in the field by the dark long pterostigma. There is no particularly close relationship to any other *Subilla* species.

Biology and ecology. So far larvae were found exclusively under the bark of *Quercus pubescens*. Only known from the type locality – a light oak forest – at 1050 m. Adults: V–VI.

Records on Mediterranean islands (Fig. 10b). Sardinia. The species is endemic to Sardinia, possibly it occurs also in Corsica. Syntopic Raphidioptera: *Fibla maclachlani*.

Biogeography. Stationary Tyrrhenian faunal element.

***Subilla colossea* (H. Aspöck, U. Aspöck & Rausch, 1979)**

Raphidia (*Subilla*) *colossea* H. Aspöck, U. Aspöck & Rausch, 1979 (odescr); H. Aspöck et al. 1991 (mon).

Subilla colossea (H. Aspöck, U. Aspöck & Rausch, 1979): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Horstmann 1993 (paras); Horstmann 1994 (paras); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); Pantaleoni et al. 2005 (tax); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). The species belongs to the *physodes*-group of the genus. It can easily be identified by characters of the male and female genitalia.

Biology and ecology. Larvae exclusively corticolous on *Pinus* and (rarely) on *Quercus ilex* in light pine forests from 200 to 750 m asl. Development (at least) two or three years. Last hibernating stage: full-grown larva. Adults: (IV)–V.

Records on Mediterranean islands (Fig. 10b). Endemic to Rhodes, probably distributed all over the island. Syntopic Raphidioptera: *Phaeostigma* (*Aegeoraphidia*) *prophetica*, *Raphidia* (*R.*) *ambigua*.

Biogeography. Stationary Anatolopontomediterranean faunal element.

***Ulrike* H. Aspöck, 1968**

Ulrike H. Aspöck, 1968 (odescr) (described as subgenus of *Raphidia* L.) [type species by original designation: *Agulla attica* H. Aspöck & U. Aspöck, 1967a]; H. Aspöck et al. 1989 (biogeogr, distr, ill: distrmap); H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol); Haring et al. 2011 (phyl); U. Aspöck et al. 2012 (fig: phyltree); H. Aspöck and U. Aspöck 2013 (cat, etymol, phyl), 2014 (cat).

Taxonomy and systematics. H. Aspöck et al. (1991), Haring et al. (2011). *Ulrike* is a conspicuous genus markedly differentiated from all other genera of the family by eidonomic characters as well as by those of the (particularly male) genitalia. It comprises two closely related species occurring in eastern parts of the Mediterranean region. In a molecular phylogenetic analysis (Haring et al. 2011) *Subilla* has emerged as the sister taxon of *Ulrike*. Based on morphological evidence, *Subilla* is probably the sister taxon of *Tauroraphidia*, and both represent the sister of *Ulrike*.

Biology. See *Ulrike syriaca*.

Distribution. Greece (Attica), Cyprus, Near East.

***Ulrike syriaca* (Steinmann, 1964)**

Raphidilla syriaca Steinmann, 1964 (odescr): H. Aspöck et al. 1991 (mon).

Ulrike syriaca (Steinmann, 1964): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); Haring et al. 2011 (phyl, phyltree); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). *U. syriaca* (Fig. 5a) is closely related to the second species of the genus, *U. attica* (H. Aspöck & U. Aspöck), which is so far known from the mainland of Greece only. The species can easily be identified also by eidonomic characters.

Biology and ecology. Larvae probably soil-dwelling. Development two years. Last hibernating stage: full-grown larva. Adults: IV–V in light forests, particularly on pines at altitudes from 100–1500 m.

Records on Mediterranean islands (Fig. 10a). Records only from Cyprus. Syntopic Raphidioptera (in Cyprus): *Phaeostigma* (*Crassoraphidia*) *cyprica*.

Continental distribution. Lebanon, Syria, Jordan, Israel.

Biogeography. (Possibly polycentric) Syrian (-Cyprian) faunal element with low expansivity. Most probably the refugial center was primarily somewhere in the Near East, from where the species invaded (passively) Cyprus (see also *Phaeostigma* (*Crassoraphidia*) *cyprica*).

***Raphidia* Linnaeus, 1758 s.l.**

Raphidia Linnaeus, 1758 (odescr) [type species by monotypy: *Raphidia ophiopsis* Linnaeus, 1758]: H. Aspöck et al. 1989 (biogeogr, distr; ill: distrmap); H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol, paras); Haring et al. 2011 (phyl); U. Aspöck et al. 2012 (fig: phyltree; list); H. Aspöck and U. Aspöck 2013 (cat, etymol, phyl), 2014 (cat).

Taxonomy and systematics. H. Aspöck et al. (1991), Haring et al. (2011). With 18 species in three subgenera (*Raphidia* s. str.: 15 spp., *Aserbeidshanoraphidia* H. Aspöck & U. Aspöck: 1 sp., *Nigroraphidia* H. Aspöck & U. Aspöck: 2 spp.). *Raphidia* is – after *Mongoloraphidia* and *Phaeostigma* – the third largest genus of the family Raphidiidae. Only the subgenus *Raphidia* s. str. is represented on Mediterranean islands with altogether 6 species, five of these (*R. mediterranea*, *R. beieri*, *R. peterressli*, *R. mysia*, *R. ambigua*) belong to a group of more closely related species, while *R. ariadne* is somewhat isolated. In a molecular phylogenetic study (Haring et al. 2011) *Raphidia* s. l. has emerged as the sister of *Dichrostigma* + *Tjederiraphidia*, but this needs confirmation.

All species can easily be differentiated by characters of the male, partly also of female genitalia.

Biology. Larvae of some species strictly corticolous, of others partly or strictly soil-dwelling. Development in some (most?) species mainly one year, in others two (or – rarely – three) years. Last hibernating stage: full-grown larva. Adults: (III)IV–VII(VIII).

Distribution. Europe (except W- and SW-Europe), Aegean islands, Anatolia, Caucasus, N-Iran, northern and northeastern Asia.

Subgenus *Raphidia* Linnaeus, 1758, s. str.

Raphidia Linnaeus, 1758 (odescr) [type species by monotypy: *Raphidia ophiopsis* Linnaeus, 1758]: H. Aspöck et al. 1989 (biogeogr, distr; ill: distrmap); H. Aspöck et al. 1991 (mon); H. Aspöck 2002 (biol, paras); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Pretzmannia H. Aspöck & U. Aspöck, 1968 (described as a subgenus of *Raphidia* L.) [type species by original designation: *Raphidia euxina* Navás, 1915d]: H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck and U. Aspöck 2014 (cat).

***Raphidia (Raphidia) mediterranea* H. Aspöck, U. Aspöck & Rausch, 1977**

Raphidia (Raphidia) ophiopsis mediterranea H. Aspöck, U. Aspöck & Rausch, 1977 (odescr): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Popov 1993 (com); U. Aspöck et al. 1995 (ethol: cop); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); H. Aspöck 2012 (cat).

Raphidia (Raphidia) mediterranea H. Aspöck, U. Aspöck & Rausch: H. Aspöck et al. 1991 (mon); Letardi and Pantaleoni 1996 (com, rec);

H. Aspöck and U. Aspöck 2007 (biogeogr, distr); H. Aspöck and U. Aspöck 2013 (cat, etymol; ill: imag, ♂ imag), 2014 (cat); Canbulat 2014 (biogeogr, distr); Sziráki 2014 (rec); Rausch et al. 2016 (tax, rec, distr, ecol); Gruppe et al. 2017 (rec, ecol); H. Aspöck et al. 2017 (molecsyst, phyl, rec, distr, biogeogr).

Raphidia mediterranea H. Aspöck, U. Aspöck & Rausch: H. Aspöck et al. 1991 (mon); Sziráki 1993 (nom, rec; ill: distrmap, gs); Güsten 1998 (rec); Pantaleoni 2005 (com, rec); Sziráki 2010 (ill: imag); Tillier et al. 2022a (rec); Gruppe et al. 2023 (biol).

Taxonomy. H. Aspöck et al. (1991), Sziráki (1993), H. Aspöck et al. (2017) (Fig. 5b, c). This species was originally described as a subspecies of *Raphidia ophiopsis* L., from which it differs morphologically slightly in characters of the male (and also female) genitalia. Based upon considerable ecological characters *R. mediterranea* has been elevated to species rank, and later this decision was corroborated by a molecular systematic analysis (H. Aspöck et al. 2017).

Biology and ecology. Larvae (Fig. 5d) soil-dwelling, in high altitudes in Greece, at least partly, corticolous. (Larvae of the isolated population in a farm house in Upper Austria develop in the straw of the fetched roof of the old building; Gruppe et al. 2017.) Development one or two years. Last hibernating stage: full-grown larva. Adults: IV–VI(VII). The preferred habitats on altitudes below 500 m are all kinds of maquis, often with mass occurrence. In high altitudes (records at 1100 m) in light forests, also in gardens.

Records on Mediterranean islands (Fig. 11a). Skyros, Euboea, Andros, Hydra, Aegina, Naxos, Paros, Ikaria, Karpathos. Syntopic Raphidioptera species on Mediterranean islands: *Phaeostigma (Ph.) euboeica* (Euboea), *Ph. (Graecoraphidia) divina retsinata* (Euboea), *Ph. (Magnoraphidia) wewalkai* (Euboea), *Ph. (M.) flammi* (Euboea), *Ph. (Aegeoraphidia) raddai* (Ikaria), *Ph. (Ae.) karpathana* (Karpathos).

Continental distribution. Greece, Bulgaria, Romania, Hungary, Austria, Italy, NW-Anatolia.

Biogeography. Pontomediterranean faunal element, probably monocentric, with the refugium in the south of the Balkan Peninsula. We assume that the occurrence in Eastern and Central Europe, in Italy, in NW-Anatolia and also on some islands is the result of anthropogenic dispersal, possibly already in antiquity and also presently (H. Aspöck et al. 2017). The populations on Karpathos show slight differences compared to populations from other islands as well as from the continent, maybe due to an immigration long ago.

***Raphidia (Raphidia) beieri* H. Aspöck & U. Aspöck, 1964a**

Raphidia beieri H. Aspöck & U. Aspöck, 1964a (odescr): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Popov 2004 (chorol).

Raphidia schizurotergalis Bartoš, 1965 (odescr): H. Aspöck et al. 1991 (mon); H. Aspöck and U. Aspöck 2014 (cat).

Raphidia (Raphidia) beieri H. Aspöck & U. Aspöck: H. Aspöck et al. 1991 (mon); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); Popov 2001 (rec); Dobosz 2007 (distr, rec); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). *Raphidia (R.) beieri* is closely related to *R. (R.) kimminsi* (which occurs in the north of Anatolia) and *R. (R.) grusinica* (which occurs in NE-Anatolia and in the western Caucasian regions) and can be differentiated only by characters of the male genitalia. Possibly these taxa form a superspecies. A clarification of the complicated taxonomic situation will only be possible by molecular systematic analyses.

Biology and ecology. Euryoecious! Larvae corticolous and soil-dwelling; many records under bark of *Abies*, *Pinus*, *Quercus*, *Pyrus* and *Prunus*, and in the litter around roots of bushes. Development usually two years, rarely one or three years. Last hibernating stage: full-grown larva. Adults: IV–VI. In various habitats – light forests with conifers as well as with only deciduous trees in altitudes from 100–1700 m. On Thasos in light pine forests with *Rosa*, *Prunus*, *Crataegus*, *Juniperus* in 900–1100 m asl., on Samothraki in pastures with single old oak trees in 1200 m asl.

Records on Mediterranean islands (Fig. 11a). Thasos, Samothraki. Syntopic species of Raphidioptera on Thasos: *Phaeostigma (Pontoraphidia) setulosa aegea*, *Venustoraphidia nigricollis*.

Continental distribution. Northeastern parts of Greece, North Macedonia, Kosovo, Bulgaria, Romania, Moldavia, Ukraine, NW-Anatolia.

Biogeography. Polycentric Pontomediterranean faunal element. Phylogeographic studies are urgently needed.

***Raphidia (Raphidia) peterressli* H. Aspöck & U. Aspöck, 1973**

Raphidia (Raphidia) peterressli H. Aspöck & U. Aspöck, 1973 (odescr): H. Aspöck et al. 1991 (mon); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Raphidia peterressli H. Aspöck & U. Aspöck: H. Aspöck et al. 1989 (biogeogr, distr).

Taxonomy. H. Aspöck et al. (1991). Probably an insular isolate of *R. ambigua*, clearly differentiated by characters of the male genitalia, a molecular systematic analysis in comparison with *R. ambigua* and other species of *Raphidia* s. str. is, however, needed.

Biology and ecology. Larvae not yet described, probably mainly soil-dwelling, but findings of a few larvae under bark of *Pistacia lentiscus*. Development probably similar to that of the closely related species. Euryoecious! Records in almost all types of vegetations with trees or bushes (pine-forests, olive-yards, all types of maquis) in altitudes from 0–1000 m.

Records on Mediterranean islands (Fig. 11a). So far only known from the island of Chios. Syntopic Raphidioptera: *Phaeostigma (Aegeoraphidia) raddai*.

Continental distribution. No records.

Biogeography. Probably endemic to Chios and thus an extremely stationary Anatolopontomediterranean faunal element.

***Raphidia (Raphidia) mysia* H. Aspöck, U. Aspöck & Rausch, 1991**

Raphidia (Raphidia) mysia H. Aspöck, U. Aspöck & Rausch, 1991 (mon, odesr): H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). Eidonomically very similar and closely related to several other species of the genus (*R. beieri*, *R. ambigua*); by characters of the male genitalia, however, easily to be identified.

Biology and ecology. Larvae at least also corticolous (findings on oak), but probably mainly soil-dwelling. Development two years. Last hibernating stage: full-grown larva. Adults: V(–VI). Euryoecious! Often high population densities in various habitats (e.g. light forests, pastures with small areas of shrubs) and on different plants: *Pistacia terebinthus*, *Pistacia lentiscus*, *Phillyrea trifolia*, *Pinus halepensis*.

Records on Mediterranean islands (Fig. 11a). So far only on Lesbos. Syntopic Raphidioptera (on Lesbos): *Phaeostigma (Aegeoraphidia) raddai*.

Continental distribution. NW-Anatolia.

Biogeography. Stationary Anatolopontomediterranean faunal element.

***Raphidia (Raphidia) ambigua* H. Aspöck & U. Aspöck, 1964b**

Raphidia ambigua H. Aspöck & U. Aspöck, 1964b (odescr): H. Aspöck et al. 1991 (mon); H. Aspöck et al. 1989 (biogeogr, distr).

Raphidia (Raphidia) ambigua H. Aspöck & U. Aspöck: H. Aspöck et al. 1991 (mon); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); Canbulat and Özşaraç 2004 (distr, rec); Canbulat and Kiyak 2006 (distr, rec; ill: map); Dobosz 2007 (distr, rec); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). The species is closely related to the other species of this group within the subgenus *Raphidia* s. str., but can easily be identified by characters of the male genitalia. There is no island on which a second *Raphidia* species besides *R. ambigua* occurs, therefore, it cannot be confused with other species of *Raphidia*.

Biology and ecology. Larvae corticolous on conifers and deciduous trees as well as soil-dwelling. Development one year. Last hibernating stage: full-grown larva.

Adults: (IV)V–VI(VII). Euryoecious! In various habitats: light (mixed) pine forests, oak forests, bush-forests, fruit-gardens, in maquis of various structure, usually in high population densities, in altitudes of 200 to 1600 m.

Records on Mediterranean islands (Fig. 11a). Samos, Rhodes. Syntopic Raphidioptera on islands: *Phaeostigma* (*Aegeoraphidia*) *raddai* (Samos), *Ph. (Ae.) prophetica* (Rhodes), *Subilla colossea* (Rhodes), *Parainocellia resslie* (Samos).

Continental distribution. Most parts of Anatolia, from the Mediterranean coast until the east.

Biogeography. Monocentric Anatolopontomediterranean faunal element with high expansivity.

Raphidia (*Raphidia*) *ariadne* H. Aspöck & U. Aspöck, 1964a

Raphidia ariadne H. Aspöck & U. Aspöck, 1964a (odescr): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); U. Aspöck et al. 2012 (fig: imag).

Raphidia (*Raphidia*) *ariadne* H. Aspöck & U. Aspöck: H. Aspöck et al. 1991 (mon); Popov 1992 (biogeogr); H. Aspöck et al. 2001 (anncat); Tröger 2005a (rec); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2013 (cat, etymol, ill: ♀ imag, ♂ imag), 2014 (cat); Sziráki 2014 (rec).

Taxonomy. H. Aspöck et al. (1991). A very conspicuous species (Fig. 5e, f), somewhat isolated within the subgenus *Raphidia* s. str., it can hardly be confused with any other species of the family.

Biology and ecology. Larvae (Fig. 5g) mainly soil-dwelling, but also corticolous: several findings of larvae and pupae under bark of *Pyrus* on the Omalos Plateau (1000–1100 m). Development one or two years. Last hibernating stage: full-grown larva. Adults: IV–VI. Euryoecus! In almost all habitats with coniferous or deciduous trees or bushes all over the island of Crete from sea level to (at least) 1550 m. Usually high population densities.

Records on Mediterranean islands (Fig. 11a). Endemic to Crete. No records from elsewhere. Syntopic Raphidioptera: *Phaeostigma* (*Aegeoraphidia*) *biroi*, *Phaeostigma* (*Superboraphidia*) *minois*, *Fibla* (*Reisserella*) *pasiphae*.

Biogeography. Monocentric Cretan faunal element.

Dichrostigma Navás, 1909

Dichrostigma Navás, 1909 (described as a section of *Raphidia* L.) [type species by subsequent designation: *Raphidia flavipes* Stein, 1863]: H. Aspöck et al. 1989 (biogeogr, distr; ill: distrmap); H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol, paras); Haring et al. 2011 (phyl); U. Aspöck et al. 2012 (fig: phyltree); H. Aspöck and U. Aspöck 2013 (cat, etymol, phyl), 2014 (cat).

Lesna Navás, 1915b (odescr) [type species by original designation: *Raphidia adanana* Albarda, 1891]: H. Aspöck et al. 2001 (anncat).

Taxonomy and systematics. H. Aspöck et al. (1991). *Dichrostigma* is a markedly differentiated genus. In a molecular phylogeny analysis (Haring et al. 2011) it has emerged as the sister group of *Tjederiraphidia* and both are the sister of *Raphidia*. *Dichrostigma* comprises four species, which can easily be differentiated also by eidonomic characters.

Biology and ecology. Larvae soil-dwelling. Development two years. Last hibernating stage: full-grown larva. Adults: IV–VII. Euryoecious. In light pine forests as well as in habitats with deciduous trees or bushes only, in altitudes from sea level to 1800 m.

Distribution. Central-, E-, SE-Europe, Anatolia, Near East. One species occurs on Mediterranean islands.

Dichrostigma flavipes (Stein, 1863)

Raphidia ophiopsis var. e: Schummel, 1832 (descr, distr): H. Aspöck et al. 1991 (mon).

Raphidia affinis Schneider, 1843 (odescr, ecol, distr): Novak 1891 (rec); H. Aspöck et al. 1991 (mon). – Homonym!

Raphidia flavipes Stein, 1863 (odescr): H. Aspöck et al. 1991 (mon); Dobosz 1989 (rec); Dobosz 1994 (rec).

Raphidia (*Dichrostigma*) *flavipes* Stein: H. Aspöck et al. 1991 (mon); Dobosz 1991 (distr, ecol, rec; ill: map); Tröger 1993 (rec).

Subilla sulfuricosta Steinmann, 1963 (odescr): H. Aspöck et al. 1991 (mon).

Raphidia sinica Steinmann, 1964 (odescr): H. Aspöck et al. 1991 (mon).

Raphidia maculicaput Steinmann, 1964 (odescr): H. Aspöck et al. 1991 (mon).

Raphidia dichroma Steinmann, 1964 (odescr): H. Aspöck et al. 1991 (mon).

Raphidia durmitorica Steinmann, 1964 (odescr): H. Aspöck et al. 1991 (mon).

Raphidia monotona Steinmann, 1964 (odescr): H. Aspöck et al. 1991 (mon).

Subilla balesdenti Poivre, 1991 (odescr; ill: imag, gs, head, wings): H. Aspöck et al. 2001 (anncat).

Raphidia (*Lesna*) *flavipes* Stein: H. Aspöck et al. 1991 (mon).

Dichrostigma flavipes Stein: H. Aspöck et al. 1989 (biogeogr, distr, ill: imag); Pantaleoni 1990a (com, rec); Pantaleoni 1990c (com, rec); Pantaleoni 1990d [1993] (rec); H. Aspöck et al. 1991 (mon); Devetak 1991 (rec); Saure and Gerstberger 1991 (ecol, rec); Devetak 1992a (rec); Devetak 1992b (com); Rausch and H. Aspöck 1993 (rec, ecol); Horstmann 1994 (paras); Pantaleoni et al. 1994 (distr, rec); U. Aspöck et al. 1995 (ethol: cop); H. Aspöck and Hölzel 1996 (distr); Hellrigl and Hölzel 1996 (list, rec); Letardi and Pantaleoni 1996 (rec); Saure 1996 (biogeogr, ecol, rec); Sziráki 1996 (ecol, rec); Achtelig 1997 (ecol, rec); Wachmann and Saure 1997 (charact; fig: imag); U. Aspöck and H. Aspöck 1999 (ill: imag); Dobosz 1999 (rec); Sziráki 1999 (rec); Ábrahám 2001 (list, rec); H. Aspöck et al. 2001 (anncat); Gruppe and Schubert 2001 (ecol, rec); Vas et al. 2001 (ecol, rec); Czechowska 2002 (ecol, rec); Tröger 2002 (rec); Ábrahám et al. 2003 (rec); Dobosz 2003 (rec); Haring and U. Aspöck 2004 (phyl); H. Aspöck and U. Aspöck 2005 (distr); U. Aspöck and H. Aspöck 2005a (biogeogr); U. Aspöck and H. Aspöck 2005b (com, anat); Nicoli Aldini 2005 (rec); Tröger 2005b (rec); Gruppe 2006c (ecol, rec); Anderle and U. Aspöck 2007 (rec); U. Aspöck and H. Aspöck 2007 (ill: ♀ imag); Gruppe and Müller 2007 (ecol, rec);

H. Aspöck and U. Aspöck 2007 (biogeogr, distr); Dobosz 2007 (distr, rec; ill: map); Badano 2008 (distr, rec); Gruppe 2008 (ecol, rec); Klokočovník et al. 2010 (rec); Letardi et al. 2010 (rec); Haring et al. 2011 (phyl, phyltree); H. Aspöck and U. Aspöck 2013 (cat, etymol; ill: ♂, ♀ imag), 2014 (cat); Morinière et al. 2014 (barcode, phyl); Sziráki 2014 (rec); Tillier et al. 2022a (rec).

Taxonomy. H. Aspöck et al. (1991). The species can easily be differentiated also by eidonomic characters, particularly by the two-colored pterostigma (proximal brown, distal yellowish) (Figs 5h, 6a).

Biology and ecology. Larvae (Fig. 6b) exclusively soil-dwelling in the litter around roots of trees and bushes. Development two years. Last hibernating stage: full-grown larva. Adults: (IV)V–VII(VIII). Euryoecious, but preferring xerothermic habitats, e.g. light pine forests, but also biotopes free of conifers.

Records on Mediterranean islands (Fig. 8b). Krk, Hvar, Korfu. Syntopic Raphidioptera on Mediterranean islands: No records.

Continental distribution. Balkan Peninsula (except southern parts of Greece), eastern Europe (till the Ural), Central Europe, northern Italy.

Biogeography. (Probably monocentric) Balkanopontomediterranean faunal element with high expansivity.

Family Inocelliidae Navás, 1913

Family Inocelliidae Navás, 1913: H. Aspöck et al. 1991 (mon), H. Aspöck and U. Aspöck 1991 (overv); H. Aspöck et al. 2001 (ann-cat); H. Aspöck 2002 (biol); H. Aspöck and U. Aspöck 2009 (overv); U. Aspöck and H. Aspöck 2009 (overv); H. Aspöck et al. 2012 (overv); Oswald and Machado 2018 (overv); Shen et al. 2022 (phyl).

Fibla Navás, 1915

Fibla Navás, 1915b (odescr) [type species by original designation: *Fibla hesperica* Navás, 1915]: H. Aspöck et al. 1989 (distr); H. Aspöck 1990 (biogeogr, distr, synlist; ill: map); H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); U. Aspöck and H. Aspöck 1994 (biogeogr); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (biol, paras); Monserrat and Papenberg 2010 (chorol); Haring et al. 2011 (phyl); H. Aspöck et al. 2012 (com); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat); Monserrat and Papenberg 2015 (overv); Shen et al. 2022 (phyl).

Taxonomy and systematics. H. Aspöck et al. (1991), Haring et al. (2011). Systematic position within the family not yet definitely resolved, however, see Shen et al. (2022). It comprises two subgenera, *Fibla* s. str. (with 3 species) and *Reisserella* (with 1 species). Both subgenera are represented on Mediterranean islands.

Biology and ecology. Larvae are exclusively corticolous on various trees. Development at least two, usually three (or more) years. Last hibernating stage: full-grown larva. Adults: IV–VII.

Distribution. Iberian Peninsula, Tyrrhenic islands, Sicily, Apennine Peninsula (sporadically), Crete, N-Africa.

Subgenus *Fibla* Navás, 1915, s. str.

Subgenus *Fibla* Navás, 1915b (odescr) [type species by original designation: *Fibla hesperica* Navás, 1915]: H. Aspöck et al. 1989 (biogeogr, distr; ill: distrmap); H. Aspöck 1990 (biogeogr, distr, synlist; ill: map); H. Aspöck et al. 1991 (mon); H. Aspöck et al. 2001 (ann-cat); H. Aspöck 2002 (biol, paras); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat); Monserrat and Papenberg 2015 (overv); Shen et al. 2022 (phyl).

Burcha Navás, 1915b (odescr) [type species by original designation: *Inocellia maclachlani* Albarda, 1891]: H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom).

Estoca Navás, 1919 (odescr) [type species by monotypy: *Estoca peyerimhoffi* Navás, 1919]: H. Aspöck et al. 1991 (mon).

Taxonomy. H. Aspöck et al. (1991). *Fibla* s. str. and *Reisserella* can easily be differentiated by eidonomic characters (and, moreover, by their geographic vicariance).

Biology and ecology. See *Fibla* s.l. and *F. maclachlani*.

Distribution. Iberian Peninsula, Tyrrhenian islands, Sicily, Apennine Peninsula, N-Africa.

Fibla (Fibla) maclachlani (Albarda, 1891)

Inocellia crassicornis auct. (nec Schummel!): H. Aspöck et al. 1991 (mon). *Inocellia maclachlani* Albarda, 1891 (odescr): H. Aspöck et al. 1991 (mon).

Burcha maclachlani (Albarda): H. Aspöck et al. 1991 (mon).

Burcha sicula Navás, 1915a (odescr): H. Aspöck et al. 1991 (mon); H. Aspöck & U. Aspöck 2014 (cat).

Fibla maclachlani (Albarda): H. Aspöck et al. 1991 (mon); Letardi 1994 (distrmap, ecol, rec); Pantaleoni 2005 (com, rec); Haring et al. 2011 (phyl); Tillier et al. 2022a (rec).

Fibla (Fibla) maclachlani (Albarda, 1891): H. Aspöck et al. 1991 (mon); U. Aspöck and H. Aspöck 1994 (distr, biogeogr, ill: imag, la, map); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); Nicoli Aldini and Baviera 2001 (rec); Haring et al. 2011 (phyl); H. Aspöck et al. 2012 (distr); Nicoli Aldini et al. 2012 (rec, distr); H. Aspöck & U. Aspöck 2013 (cat, etymol; ill: la, ♂ imag), 2014 (cat); Pantaleoni et al. 2019 (distr, ecol, rec); Shen et al. 2022 (phyl).

Taxonomy. H. Aspöck et al. (1991). A very characteristic species (Fig. 6c, d) and the only representative of the family on the Tyrrhenian islands and in Sicily.

Biology and ecology. Larvae (Fig. 6e) exclusively corticolous, mainly on *Pinus*, but often also on deciduous trees (*Amygdalus*, *Quercus*). Preferred biotopes: Light pine and oak forests, but also in wild fruit gardens. Records from 150–1600 m; probably also occurring at sea level.

Records on Mediterranean islands (Fig. 11b). Corsica, Sardinia, Sicily. Syntopic occurrence with other Raphidioptera: *Xanthostigma corsica* (Corsica, Sardinia, Sicily), *Xanthostigma aloysiana* (Sardinia), *Subilla confinis* (Sicily), *Subilla principiae* (Sardinia). Development:

Three or more years. Last hibernating stage: full-grown larva. Adults: IV–VI.

Continental distribution. Apennine Peninsula, probably introduced from Sardinia with cork; old and recent records in Calabria need confirmation (Pantaleoni et al. 2019).

Biogeography. Polycentric (?) stationary Tyrrhenian-(Adriatomediterranean?) faunal element.

Subgenus *Reisserella* H. Aspöck & U. Aspöck, 1971

Reisserella H. Aspöck & U. Aspöck, 1971 (odescr) (described as a subgenus of *Inocellia* Schneider) [type species by original designation: *Inocellia (Reisserella) pasiphae* H. Aspöck & U. Aspöck, 1971]: H. Aspöck et al. 1989 (distr); H. Aspöck 1990 (biogeogr, distr; ill: map); H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2012 (cat); H. Aspöck et al. 2012 (distr); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat); Shen et al. 2022 (phyl).

Taxonomy. H. Aspöck et al. (1991). Easily to be differentiated from *Fibla* s.str. by eidonomic and by genitalic characters. Only one species known.

Biology and ecology. See *Fibla (Reisserella) pasiphae*.

Distribution. Endemic to Crete.

Fibla (Reisserella) pasiphae (H. Aspöck & U. Aspöck, 1971)

Fibla sp.: H. Aspöck & U. Aspöck, 1966 (tax, distr). H. Aspöck et al. 1991 (mon).

Inocellia (Reisserella) pasiphae H. Aspöck & U. Aspöck, 1971b (odescr): H. Aspöck et al. 1991 (mon).

Fibla elkeweimarae Lauterbach, 1972 (odescr): H. Aspöck et al. 1991 (mon); H. Aspöck and U. Aspöck 2014 (cat).

Fibla (Reisserella) pasiphae (H. Aspöck & U. Aspöck): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); Popov 1992 (biogeogr); U. Aspöck and H. Aspöck 1994 (biogeogr; ill: distrmap); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); Tröger 2005a (rec); H. Aspöck 2012 (cat); H. Aspöck et al. 2012 (distr; fig: imag, la, pu); H. Aspöck and U. Aspöck 2013 (cat, etymol; ill: ♀ imag, la, ♂ imag, pu), 2014 (cat); Shen et al. 2022 (ill: ♀ imag, phyl).

Taxonomy. H. Aspöck et al. (1991). Easily recognized (Fig. 6f, g), moreover, it is the only Inocelliid species occurring in Crete.

Biology and ecology. Larvae (Fig. 6h) corticolous on various deciduous trees (*Amygdalus*, *Pyrus*), probably also on *Pinus*. Occurs in various habitats of light forests, wild gardens, and in various types of maquis with single trees in altitudes from sea level to (at least) 1200 m. Development (at least) two years. Last hibernation stage: full-grown larva. Adults: IV–VI.

Records on Mediterranean islands (Fig. 11b). Distributed all over Crete, but confined to this island. Syntopic other Raphidioptera: *Phaeostigma (Aegeoraphidia) biroi*, *Ph. (Superboraphidia) minois*, *Raphidia (R.) ariadne*.

Biogeography. Endemic to Crete. Monocentric Cretan faunal element.

Parainocellia H. Aspöck & U. Aspöck, 1968

Parainocellia H. Aspöck & U. Aspöck, 1968 (odescr) (described as a subgenus of *Inocellia* Schneider) [type species by original designation: *Inocellia resslis* H. Aspöck & U. Aspöck, 1965b]: H. Aspöck et al. 1991 (mon); Oswald and Penny 1991 (cat, nom); H. Aspöck et al. 2001 (anncat); H. Aspöck 2002 (paras); Liu et al. 2009 (syst); Haring et al. 2011 (phyl); H. Aspöck 2012 (cat); H. Aspöck et al. 2012 (distr); H. Aspöck and U. Aspöck 2013 (cat, etymol), 2014 (cat); Shen et al. 2022 (phyl).

Taxonomy and systematics. H. Aspöck et al. (1991), Liu et al. (2009). *Parainocellia* comprises presently three species which are eidonomically similar to each other and to other species of Inocelliidae presently in the genus *Inocellia*. By morphological characters of the male genitalia they can, however, easily be identified.

Biology and ecology. Larvae corticolous on many coniferous as well as deciduous trees from sea level to (at least) 1200 m. Development at least two or three years. Last hibernating stage: full-grown larva. Adults: V–VII(VIII).

Distribution. Apennine Peninsula, Balkan Peninsula, Central and Eastern Europe, Samos, Anatolia.

Parainocellia resslis (H. Aspöck & U. Aspöck, 1965b)

Inocellia resslis H. Aspöck & U. Aspöck, 1965b (odescr): H. Aspöck et al. 1991 (mon); Shen et al. 2022 (phyl, ill: ♂ gs).

Inocellia (Parainocellia) resslis H. Aspöck & U. Aspöck: H. Aspöck et al. 1991 (mon).

Parainocellia resslis (H. Aspöck & U. Aspöck): H. Aspöck et al. 1991 (mon); H. Aspöck and U. Aspöck 1991 (ill: head, wings, ♂ gs); H. Aspöck et al. 2012 (distr); H. Aspöck and U. Aspöck 2013 (cat, etymol).

Parainocellia (Parainocellia) resslis (H. Aspöck & U. Aspöck): H. Aspöck et al. 1989 (biogeogr, distr); H. Aspöck et al. 1991 (mon); H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (anncat); U. Aspöck and H. Aspöck 2005b (ill: head, prothorax, pterothorax, tarsalia); Canbulat and Kiyak 2006 (distr, rec; ill: map); U. Aspöck and H. Aspöck 2007 (ill: head, la); Dobosz 2007 (distr, rec); H. Aspöck 2012 (cat); H. Aspöck and U. Aspöck 2014 (cat).

Taxonomy. H. Aspöck et al. (1991). Eidonomically very similar to *Parainocellia braueri* (Balkan Peninsula, south-east of Central Europe, Eastern Europe) and to *P. bicolor* (Apennine Peninsula, southwest of Central Europe), but easily to be identified by characters of the male genitalia.

Biology and ecology. Larvae corticolous on *Pinus*, *Quercus* (and probably many other trees). Typical habitats: light pine forests and mixed pine-oak forests, also on single old trees, e.g. in pastures from sea level to (at least) 1800 m. Development: at least three (possibly also two) years. Last hibernation stage: full-grown larva. Adults: V–VII.

Records on Mediterranean islands (Fig. 11b). Samos. Syntopic Raphidioptera on Samos: *Phaeostigma (Aegeoraphidia) raddai*, *Raphidia (R.) ambigua*.

Continental distribution. South and east Anatolia.

Biogeography. Monocentric Anatoloponotmediterranean faunal element with low expansivity.

Discussion

The Raphidioptera of the Mediterranean islands in the mirror of the Raphidioptera of the world

Presently we know 252 described valid species of the order Raphidioptera: 206 species of Raphidiidae and 46 species of Inocelliidae. Fig. 12a, c shows the distribution of these species in the world (see also Fig. 1). The Mediterranean region, as well as Central and Eastern Asia, are known hotspots of biodiversity (Myers et al. 2000), which is also reflected by the distribution of Raphidioptera. By far most snakefly species occur in Europe and in the Middle East (115 species = 45,6% of the world fauna), and of these 33 species = 13,1% of the world fauna inhabit Mediterranean islands. 99 species occur in Central Asia or Eastern Asia, i.e. 39,3% of the world fauna.

Only 5 species (= 2%) have so far been found in Africa (restricted to the northwestern parts of the conti-

nent). America (a relatively small part of North America only: see Fig. 1) harbors 32 species (= 12,7% of the world fauna).

Fig. 12b, d shows the significance of Raphidioptera occurring on Mediterranean islands compared to the total numbers of Raphidioptera, Raphidiidae and Inocelliidae respectively within the whole Mediterranean region, i.e. all countries of Europe, Asia, and Africa bordering the Mediterranean Sea.

Geographical definitions: Middle East comprises Turkey, Cyprus, Syria, Lebanon, Jordan, Israel, Armenia, Georgia, Azerbaijan, Iraq, Iran, and Afghanistan. Central Asia comprises Kazakhstan, Kyrgyzstan, Uzbekistan, Tajikistan, Pakistan, northern India, and Mongolia. East Asia comprises the East Asian part of Russia, China, Taiwan, Japan, Myanmar, and Thailand. In America Raphidioptera occur in Canada, USA, and Mexico.

How have the Mediterranean islands been colonized by Raphidioptera?

Tables 1, 2 give an overview of the 33 species of Raphidioptera recorded from Mediterranean islands and of the 28 islands with confirmed occurrence of certain snakefly species. How and when have these 33 snakefly species come to the islands or have some of them ever been there?

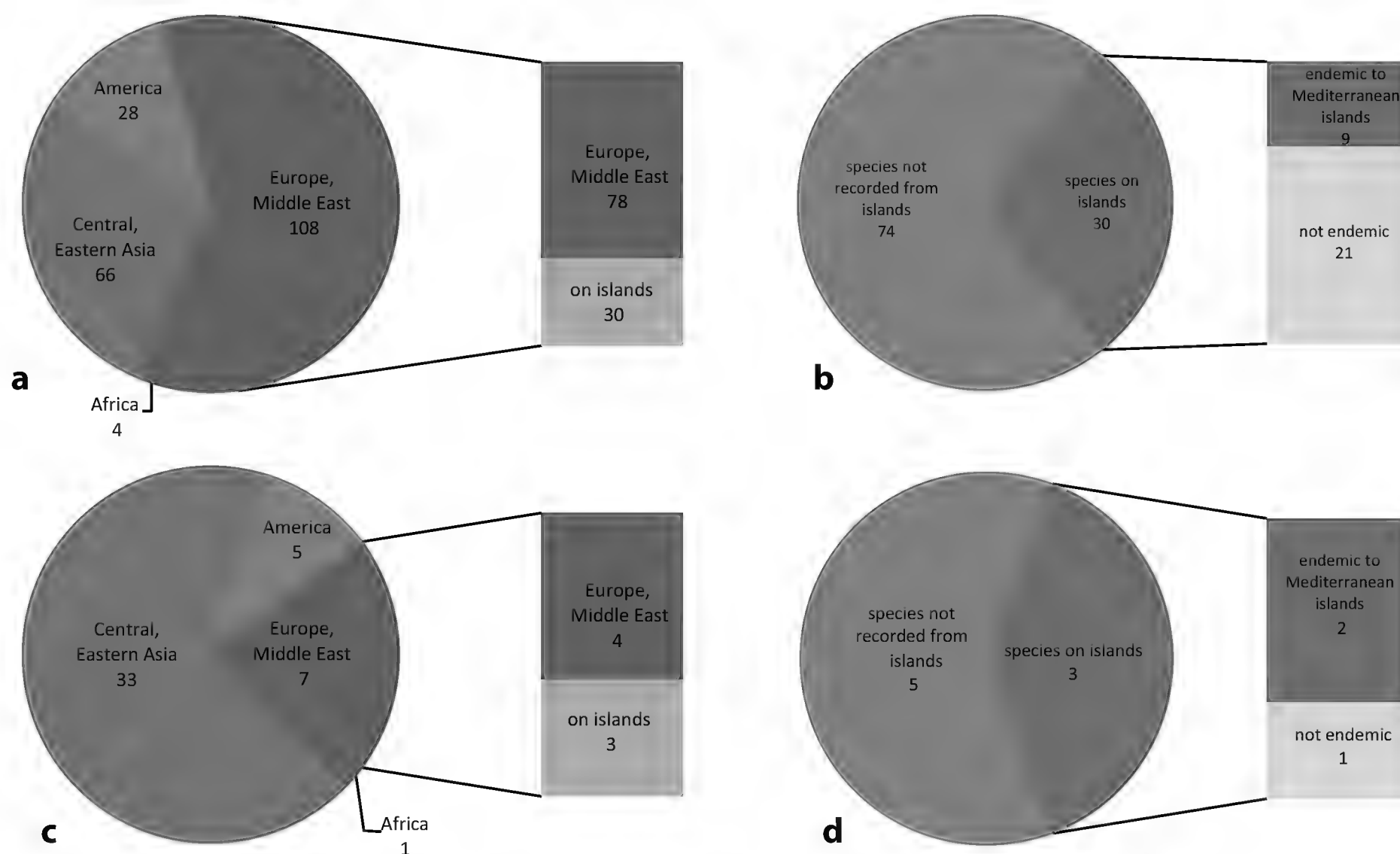


Figure 12. The Raphidioptera of the Mediterranean region **a.** Raphidiidae of the world (206 spp.). Two species (*Raphidia ophiopsis* and *Xanthostigma xanthostigma*) occur in Europe, Northern Asia, and Far East. In this graph they are included only in Europe and therefore counted only once; **b.** Raphidiidae of the Mediterranean region (104 spp.); **c.** Inocelliidae of the world (46 spp.). One species (*Inocellia crassicornis*) occurs in Europe, Northern Asia, and Far East. In this graph it is included only in Europe and therefore counted only once; **d.** Inocelliidae of the Mediterranean region (8 spp.).

The palaeogeography of the Mediterranean islands is very diverse – a fact which is impressively reflected also by their diverse Raphidioptera fauna. The most important factors are origin, emergence, age, and development of the different islands on one hand and whether they had connections to continental areas during the Pleistocene or whether they have been isolated for long periods, on the other hand. The desiccation by evaporation of the Mediterranean Sea between 5 and 6 mya led to many land bridges but these were of no major significance for the dispersal of the snakeflies as the dried-up areas were largely covered by evaporates or had the characters of lagoons.

Here we try to analyze the origin of the Raphidioptera fauna of those Mediterranean islands where snakeflies have been found:

Tyrrhenian islands

The Tyrrhenian islands Sardinia and Corsica were separated from the Iberian Peninsula in the Oligocene more than 32 mya and since that time never connected with continental Europe. In the Pleistocene, i.e. during 2.5 mya, they were repeatedly connected to each other for several 10,000 years so that an extensive exchange of organisms could occur. In Corsica two snakefly species have been found (*Xanthostigma corsica* and *Fibla* (F.) *maclachlani*), in Sardinia four species (*X. corsica*, *X. aloysiana*, *Subilla principiae*, and *F. (F.) maclachlani*). *X. corsica* occurs also on islands of the Tuscany archipelago (Elba, Giglio) and in Sicily. Moreover, the species is widely distributed in the Apennine Peninsula, in the southeast of France and also in isolated areas in Spain (H. Aspöck et al. 1991). The most closely related species are *X. aloysiana* and *X. xanthostigma* (Schummel, 1832), both occurring in large parts of the continent, *X. aloysiana* in Italy, S-Switzerland, France and NE-Spain, *X. xanthostigma* as a Eurosibirian species from Europe to the Far East (H. Aspöck et al. 1991). It is thus a reasonable assumption that *X. corsica* has reached the islands by dispersal from the continent. When these invasions to Sardinia, Corsica, and other islands may have occurred, is unknown. The situation with *X. aloysiana* is very similar.

A third species of the family Raphidiidae occurring in Sardinia was detected at the beginning of this century: *Subilla principiae*. The species is rather isolated within the genus, and the sister taxon cannot be identified. *S. principiae* is endemic to Sardinia (perhaps it can be found also in Corsica) and it is certainly a very old Tyrrhenian faunal element. When and how it has come to Sardinia, is, however, unknown. The Iberian Peninsula harbors a *Subilla* species, *S. aliena* (Navás, 1915), but this species is closely related to *Subilla confinis* (Stephens, 1836), which is an expansive Adriatomediterranean faunal element. Moreover, all other *Subilla* species are Ponto-mediterranean faunal elements distributed in the Balkan Peninsula or in Anatolia. It is therefore unlikely, one can even exclude that *S. principiae* is of Iberian origin; the more enigmatic is the presence of this Tyrrhenian *Subilla* species in Sardinia. The fourth species of Raphidioptera

occurring in Sardinia (and Corsica), *Fibla* (F.) *maclachlani*, is clearly of Iberian origin and thus a very old faunal element in Corsardinia. It occurs also in Sicily, but primarily not in the Italian mainland and can thus be regarded as an endemism of Corsardinia and Sicily. However, in recent years it has been introduced to the mainland by human activities when cork was brought from Sardinia to Tuscany (Pantaleoni et al. 2019). *Fibla* (F.) *maclachlani* is closely related to *Fibla* (F.) *hesperica*, which is widely distributed on the Iberian Peninsula. Together with *Fibla* (F.) *peyerimhoffi* (Navás, 1919), which is known from various parts of N-Morocco, N-Algeria, and N-Tunisia, they form the subgenus *Fibla* Navás, 1915. One may assume that in the Oligocene when the landmasses which later formed Corsica and Sardinia got separated from Iberia they took the ancestors of the extant *Fibla* (F.) *maclachlani* with them into the insular isolation.

Adriatic and Ionian islands

The islands in the Adriatic Sea as well as those in the Ionian Sea had connections to the continent, i.e. the Balkan Peninsula, during the Pleistocene. This led to an immigration of species from the continent into the former islands.

The Raphidioptera fauna of the islands of Krk, Hvar, Korfu, Levkas, and Kefalonia comprises only snakefly species which occur also in the adjacent continent: *Dichrostigma flavipes* (Krk, Hvar, Korfu), *Parvoraphidia microstigma* (Levkas), *Ornatoraphidia flavilabris* (Levkas), *Subilla artemis* (Levkas), *Phaeostigma* (*Magnoraphidia*) *major* (Levkas, Kefalonia).

Northern and western Aegean islands

Also the islands of the Northern Aegean Sea harbor only snakefly species of the adjacent continental regions, to which they were connected by land bridges in the Pleistocene: *Phaeostigma* (*Pontoraphidia*) *setulosa aegea* (Thasos), *Raphidia* (R.) *beieri* (Thasos, Samothraki), *Venustoraphidia nigricollis* (Thasos).

Among the Sporades only Skopelos and Skyros have been investigated for Raphidioptera. Skopelos harbors *Phaeostigma* (*Magnoraphidia*) *flammi*, a species which had been described from Euboea, but later had been found in the Pilion mountains on the continent. Euboea, Skopelos and the other Sporades and the continental area where the Pilion mountains are situated were connected to one land mass in the Pleistocene.

On the island of Skyros so far only one snakefly species has been found: *Raphidia mediterranea*, which also occurs in the adjacent continental parts of Greece and in Euboea.

The large island of Euboea with high mountains (up to almost 1800 m) in the north, in the center, and in the south harbors (at least) six snakefly species: *Ornatoraphidia christianodagmara*, *Phaeostigma* (Ph.) *euboica*, Ph. (*Graecoraphidia*) *divina retsinata*, Ph. (*Magnoraphidia*) *flammi*, Ph. (M.) *wewalkai*, and *Raphidia* (R.) *mediterranea*. During the Pleistocene Euboea was repeatedly widely connected with continental Greece for long periods so that

there must have been an intensive faunal exchange. It is thus surprising that one of the six species of the snakeflies of Euboea, *Ph. euboica*, has so far not been found outside the island and has therefore until now been regarded as an endemism of Euboea. Another species of the subgenus *Phaeostigma*, *Ph. (Ph.) pilicollis* (Stein), is distributed all over Greece. The sister taxon to *Ph. euboica* is, however, not *Ph. pilicollis*, but the species of the *Ph. notata* group of the subgenus which occur in Northern parts of the Balkan Peninsula, in the Apennine Peninsula, and large parts of East, Central, and West Europe. *Ph. euboica* must therefore be an older isolate (possibly early Pleistocene).

Ph. (G.) divina retsinata was primarily thought to be endemic to Euboea, but was later found in two further isolated populations in two mountain ranges in Attika (Parnis, Pateras). The other two subspecies of *Ph. (G.) divina*, *Ph. d. divina* and *Ph. d. simillima*, are confined to small areas in continental Greece north of the Gulf of Korinthos. Two other species of the subgenus *Graecoraphidia*, *Ph. (G.) hoelzeli* H. Aspöck & U. Aspöck, 1964, and *Ph. (G.) albarda* Rausch & H. Aspöck, 1991, occur in small isolated areas in the north of the Peloponnisos. All species of *Graecoraphidia* are old Balkanopontomediterranean faunal elements of a very low expansivity, which were confined to Greece probably throughout the whole Pleistocene.

Euboea harbors two species of *Magnoraphidia*: *Phaeostigma (M.) flammi* and *Ph. (M.) wewalkai*. Both species occur in restricted areas of the adjacent continental region, from where they may have colonized Euboea in the Pleistocene. *Ornatoraphidia christianodagmara* is so far known from two localities, Parnis mountain in Attica (850–1120 m) and Ochi mountain range in the south of Euboea (1100 m). Probably the species has reached Euboea from the adjacent continental regions in one of the glacial periods.

The genus *Ornatoraphidia* comprises only one further species: *O. flavilabris*, which occurs in many parts of Greece, however, neither in Euboea nor in Attica.

Raphidia (R.) mediterranea is a Balkanopontomediterranean faunal element, which has been probably introduced from its primary refugial centers (in Greece) to other parts of the Balkan Peninsula and to Aegean islands, but also to Italy and even to Central Europe, probably mainly by anthropogenic dispersal and perhaps already in antiquity (H. Aspöck et al. 2017).

The only snakefly species so far recorded from Andros, from Aegina, and from Hydra is *Raphidia (R.) mediterranea* (see above). As regards the Kyklades, snakeflies have been found on the islands of Naxos and Paros. Naxos has been intensively investigated. Only one snakefly species has been found on each of these islands: *Raphidia (R.) mediterranea* (see above). Although the Kyklades comprise more than 30 larger (and many small) islands, it may be assumed that all these islands harbor very few snakeflies, possibly only *R. mediterranea*. Since the formation of the Aegean Sea due to tectonic events about 10 mya the islands had repeated connection to one another or were overflowed and emerged again, and none of the Kyklades remained isolated for

a sufficiently long time to allow the formation of a stable snakefly fauna. Moreover, all these islands lack high mountains, which are an important precondition for the formation of refugial subcenters.

Crete

A totally different situation pertains to the island of Crete. Also, Crete originated when the Aegean Sea was formed. It was and is the southernmost part of Europe. And since its formation Crete remained isolated. It was often partly overflowed, but parts of the island always remained so that the original fauna of the island (at least the majority) could always survive throughout the past for ca. 10 million years. This is why Crete harbors so many endemic animals and plants. Crete harbors four snakefly species – three species of the family Raphidiidae and one Inocelliid species – all of them are endemic to Crete and have not been found elsewhere. Are they the descendants of the old fauna after the origin of Crete? Or have they, or some of them, or their ancestors reached Crete from elsewhere? It is and it will probably not be possible to answer these questions, however, one can at least try to find out the nearest relatives of these species which is always a challenging task of phylogeography.

Phaeostigma (Aegeoraphidia) biroi is related to *Ph. (Ae.) karpathana* (endemic to Karpathos), *Ph. (Ae.) prophetica* (endemic to Rhodes), *Ph. (Ae.) resli* (SW-Anatolia), and *Ph. (Ae.) vartianorum* (SW-Anatolia). The whole subgenus is of distinct Anatolian origin, but it remains unknown how and when (the ancestors of) the species have come to Crete. Before the development of the Aegean Sea Greece and Anatolia formed one large land mass. *Phaeostigma (Superboraphidia) minois* (known only in a few specimens from a few localities in the Levka mountains in the west of Crete) seems systematically isolated and has been assigned to the subgenus *Superboraphidia* with some hesitation. *Superboraphidia* comprises four more species, three of them occurring in small areas in high elevations in Greece (*Ph. auberti* (H. Aspöck & U. Aspöck, 1966), *Ph. rauschi* (H. Aspöck & U. Aspöck, 1970), *Ph. mammaphila* (H. Aspöck & U. Aspöck, 1974)) and in the west of Anatolia (*Ph. turcica* (H. Aspöck & U. Aspöck & Rausch, 1981)); also, each of these species seems somewhat isolated within the subgenus. *Ph. (S.) minois* may be a descendant of the old fauna of Crete. The fourth snakefly species, the Inocelliid *Fibla (Reisserella) pasiphae*, represents a total conundrum. The subgenus *Fibla* is distributed in the Iberian Peninsula, Corsardinia, Sicily, and North Africa, but nowhere else. How is it possible that the sister taxon of *Fibla* s. str., i.e. *Reisserella*, occurs in Crete, entirely isolated? At first one may think of a possible land-bridge to the north of Africa in a glacial period, but according to palaeogeological evidence such a land-bridge never existed: Crete has been isolated as an island (of changing shape) since its origin about 10 mya. It is also extremely unlikely that at some point in the past larvae of a *Fibla* species (or an ancestor of a *Fibla* species) reached Crete by wood or

by swimming wood from the western part of the Mediterranean Sea. So far the question must remain open.

Karpathos

The palaeogeography of Karpathos and also – mutatis mutandis – that of Rhodes is similar to that of Crete. When the Aegean Sea developed about 10 mya Karpathos emerged as an island. Later, in the Messinian, Karpathos and Rhodes became united, but from the late Pliocene onwards Karpathos became again isolated, while Rhodes was connected with the Anatolian mainland. In the Pleistocene both islands remained isolated. This palaeogeographical history explains the snakefly fauna of Karpathos and Rhodes. Karpathos (the island has been investigated intensively by us for Raphidioptera) harbors two species of Raphidioptera, both Raphidiidae: *Phaeostigma (Aegeoraphidia) karpathana* and *Raphidia (R.) mediterranea*. *Ph. (Ae.) karpathana* is either the descendant of a species which inhabited the island already at the time of its origin or (more probably) of a species which invaded into Karpathos when the island was united with Rhodes in the Pliocene. The populations of *R. (R.) mediterranea* of Karpathos are slightly different from the populations of other parts (including islands) of Greece as well as of Italy. So far, we have hesitated to describe the Karpathos phaenon as a subspecies of *R. mediterranea* and we do not want to do it without a molecular systematic study. However, presently there is no adequately preserved material available. *R. mediterranea* has been most probably introduced from its original refugial area in Greece into many other parts of its present distribution area (H. Aspöck et al. 2017), mainly by human activities, but probably also by natural ways (e.g. swimming wood) so that the species may have reached also Karpathos at any time in the past.

Rhodos

Rhodos (Rhodos) is inhabited by three species of Raphidioptera, all Raphidiidae: *Phaeostigma (Ae.) prophetica*, *Subilla colossea*, and *Raphidia (R.) ambigua*. It is out of the question that all three species are of Anatolian origin. *R. ambigua* is widely distributed in Anatolia, from where it must have colonized Rhodes. *Ph. prophetica* and *S. colossea* are endemic to Rhodes, but the sister taxa of both species occur in Anatolia.

Eastern Aegean islands

Four islands whose Raphidioptera faunas have been investigated thoroughly have to be especially considered: Lesbos, Chios, Samos, Ikaria. All four islands were regularly connected with the Anatolian mainland during the Pleistocene and also earlier. Thus, it is not surprising that these islands do not harbor endemic species – with one exception. All four islands are inhabited by *Phaeostigma (Aegeoraphidia) raddai*, a species which occurs in

the west of Anatolia. All four islands harbor a species of *Raphidia* s. str.: Lesbos is inhabited by *Raphidia (R.) mysia*, which also occurs in the west of Anatolia, on Samos *R. (R.) ambigua* occurs, which is widely distributed in Anatolia (and in Rhodes). Ikaria is inhabited by *R. (R.) mediterranea*, a species known from many parts of Greece including several islands (see above: Euboea, Andros, Naxos, Paros, Karpathos); it has possibly been introduced to Ikaria by human activities. On the island of Chios, the subgenus *Raphidia* s. str. is, however, represented by *Raphidia (R.) peterressli*, which has so far never been found outside Chios. Is it really an endemism of Chios or is it still to be detected in Anatolia? It is of interest that all four islands harbor a different species of *Raphidia* s.str., and all four species occur on “their” island from coastal areas to the highest elevations. On the island of Samos *Parainocellia ressi* was found. The species is widely distributed in the southern parts of Anatolia almost as far as to the Iranian border.

The great Austrian botanist Karl Heinz Rechinger (1906–1998) carried out several extensive phytogeographical studies in the Aegean area (Rechinger 1950; Rechinger and Rechinger-Moser 1951) and could show that there is a biogeographical borderline between the Cyclades and the East Aegean Islands (Lesbos, Chios, Samos, Ikaria, Rhodes and the other islands of this region) separating the flora of Europe from that of Asia. Strid (1996) proposed the name “Rechinger’s Line” for this boundary. This line can convincingly be confirmed by the distribution of the Raphidioptera of the Aegean Islands.

Cyprus

Cyprus is inhabited by two snakefly species, both Raphidiidae: *Phaeostigma (Crassoraphidia) cyprica* and *Ulrike syriaca*. Both species occur in Asian countries bordering the Mediterranean Sea (Syria, Lebanon, Israel). It is surprising that none of the many Raphidioptera species occurring in the south of Anatolia have been found on the island of Cyprus which is a strong argument for the assumption that Cyprus was never connected to Anatolia. Cyprus is of Levantine origin by a submarine break off, it drifted to the west and emerged from the sea in the [late] Miocene. This means that Cyprus was without terrestrial organisms, when it appeared. It is discussed that there was a connection with the Asian continent in the late Messinian (Jolivet et al. 2006; Bache et al. 2012). In this case Cyprus could have easily received terrestrial organisms from the Levante. Otherwise, the island must have been colonized by introductions by wind or via wood drifted in the sea. At any rate, the two snakefly species presently occurring in Cyprus cannot be differentiated from individuals from the Levante morphologically. This supports the assumption of a late introduction, in the Pleistocene or even in the Holocene, possibly by human activities. The Neuropterida fauna of Cyprus is – compared to other large Mediterranean islands – moderate and comprises only three endemisms (Badano and Makris 2020), which is in agreement with

the comparatively young age of the island and the highly reduced ways of invasions by species from the continent.

Open questions in research on the Raphidioptera of the Mediterranean islands

Degree of explorations of Mediterranean islands for Raphidioptera

The Mediterranean has more than 4.300 islands, from 28 of these records of Raphidioptera are available. Is this representative? This question can be clearly affirmed. The majority of the islands of the Mediterranean Sea are small, frequently rocks of low altitude and uninhabited. Generally speaking, snakeflies need forests or forest-like habitats, preferably in higher altitudes. Lowlands harbor very few species and usually only those which occur on the adjacent mainland. The most favorable conditions for snakeflies are fulfilled in large islands with elevations of 500 to 1500 m.

Of the 28 islands with records of Raphidioptera the following islands have been specifically investigated intensively for their Neuropterida and particularly for their Raphidioptera: Corsica, Sardinia, Sicily, Levkas, Thasos, Samothraki, Skopelos, Skyros, Euboea, Naxos, Crete, Karpathos, Lesbos, Samos, Ikaria, Chios, Rhodes, Cyprus.

These 18 islands comprise – with the exception of Mallorca – the 10 largest islands of the Mediterranean. 10 islands have not been particularly investigated for Raphidioptera, but single records are available: Elba, Giglio, Krk, Hvar, Korfu, Kefalonia, Andros, Hydra, Aegina, Paros. Most of these are small and near the mainland and all of them were connected with the mainland or to each other in the Pleistocene. A few additional species may be found on some of these islands, but certainly only those which occur on the adjacent mainland and certainly no endemisms. The Aegean islands of Limnos and Syros were explored for snakeflies, however none were found. The small islands off the southern coast of Anatolia, in particular Kastelorizo (highest elevation <300 m), may harbor one or two snakefly species distributed in southern parts of Anatolia, which is characterized by a rich Raphidioptera fauna.

However, there are at least two groups of islands which must be investigated: the Balearic Islands and Malta. Probably no Raphidioptera will be found on any of the islands of Malta. The highest elevations of Malta are less than 250 m asl. *Raphidia mediterranea* could occur, if it has been introduced. There is an entirely different situation with the Balearic Islands (Mallorca, Menorca, Ibiza and Formentera). Particularly Mallorca is an island with high mountains (almost 1500 m asl.) and with large forests and forest-like habitats. The Balearic Islands were separated from the Iberian Peninsula in the Oligocene (like the later Tyrrhenian islands). One can reasonably assume that the land broken off from the mainland and having given rise to the Balearic Islands harbors the remnants of the old snakefly fauna. One might expect at least a species of *Ohmella* H.A. & U.A. (Raphidiidae) (probably undescribed) and a

species of *Fibla* (probably also undescribed). So far there are no records of Raphidioptera from the Balearic Islands.

Endemic species on Mediterranean islands

So far, endemic snakefly species have mainly been found on old islands separated from the mainland by tectonic events long ago (prior to the Pleistocene or Miocene) and have remained isolated.

- Tyrrhenian islands + Sicily (*Fibla* (F.) *maclachlani*)
- Sardinia (*Subilla principiae*)
- Crete (*Phaeostigma* (Aegeoraphidia) *biroi*, *Ph.* (Superboraphidia) *minois*, *Raphidia* (R.) *ariadne*, *Fibla* (Reisserella) *pasiphae*)
- Rhodes (*Phaeostigma* (Aegeoraphidia) *prophetica*, *Subilla colossea*)
- In addition to these eight species, two species were found on single islands only:
- *Phaeostigma* (Ph.) *euboica* on Euboea and
- *Raphidia* (R.) *peterressli* on Chios.

Both islands were connected to the adjacent mainland during the Pleistocene so that it seems unlikely that they really harbor endemic species. This pertains particularly to *R. peterressli* as this species occurs also at low elevations as well as on the mountains all over Chios. In *Phaeostigma* on Euboea there is, however, a quite different situation: The species is confined to small areas at high elevations. Possibly these areas are more or less (with shifts of vertical distribution) identical with the refugial center of this extreme stationary species during the last glacial period and possibly there were no other refugial areas. Thus, *Ph. euboica* could really be endemic to Euboea. Nevertheless, it seems strange that the most closely related species of *Ph. euboica* occur far distantly on the Balkan Peninsula.

It is rather unlikely that other islands – except the Balears – harbor endemic species so far undiscovered, but it cannot be excluded, of course.

At least on the island of Mallorca (highest elevation almost 1,500 m) Raphidioptera occur, most probably endemic species (possibly of the genera *Ohmella* and *Fibla* respectively).

Suggested molecular taxonomic and phylogeographical studies

So far all identifications of snakeflies from islands have been performed on the basis of morphological characters. All 33 species can be regarded as exactly described and there are no doubtful taxa.

Nevertheless, in a few cases molecular studies would be useful for various reasons:

- *Phaeostigma* (Graecoraphidia) *divina retsinata*: This taxon has been recorded from high altitudes in Euboea as well as in the Parnis and Pateras mountains. Other subspecies – *Ph.* (G.) *d. divina* and

Ph. (G.) d. simillima – have been described from other mountains north of the Gulf of Korinthos. It would be of interest to investigate various populations of this species from various parts of the whole distribution area.

- *Phaeostigma (Aegeoraphidia)* spp.: *Ph. (Ae.) biroi*, *Ph. (Ae.) karpathana*, *Ph. (Ae.) prophetica*. These three species belong to a group of species of the subgenus to which also several species of the Anatolian mainland have been assigned. It would be of interest to analyze the relationship of these taxa on the basis of molecular phylogeny.
- *Phaeostigma (Superboraphidia) minois*. This species endemic to Crete has been found in a small area of western Crete on the Omalos plateau in an altitude of 1000 m. Its assignment to the subgenus *Superboraphidia* was made with some hesitation. Therefore, molecular systematic studies of this and other *Superboraphidia* species and also of species of other subgenera could clarify the systematic position of *Ph. (S.) minois*.
- *Raphidia (R.) peterressli*. This species has been found so far only on the island of Chios. Chios was repeatedly connected to the Anatolian mainland during the Pleistocene, so it is unlikely that it harbors an endemic species. Comparative molecular studies with other species of the subgenus occurring on the adjacent islands and on the Anatolian mainland would be desirable.
- *Raphidia (R.) mediterranea*. This species occurs on several islands of the Aegean Sea and also in large parts of continental Greece as well as in Italy, in Eastern Europe and even in an old farmhouse in Central Europe. Comparative molecular studies of specimens from continental Greece, from Italy and from Austria have led to the conclusion that the species has been dispersed by human activities (H. Aspöck et al. 2017). So far it was not possible to study specimens from islands. This would be very interesting, particularly also with respect to the slight morphological differences found in the population of Karpathos.

It is unlikely that cryptic species will be detected on Mediterranean islands by detecting significant genomic differences compared to populations of continental regions. All these species have colonized the islands quite recently. Moreover, genetic differences without morphological correlations can hardly justify the differentiation of separate species (H. Aspöck et al. 2021).

Endangered species of Raphidioptera on Mediterranean islands

Finally, we would like to raise the question whether any of the snakefly species occurring on Mediterranean islands may be endangered. Almost all species found in a certain island are distributed all over the whole island usually in a large vertical range. Despite the fact that

many habitats are destroyed these species can survive in so many other areas that they are not endangered. There are, however, a few species which are confined to such small areas that they could possibly be eradicated if their habitats are destroyed: *Phaeostigma (Ph.) euboica* (Euboea), *Ph. (Graecoraphidia) divina retsinata* (Euboea), *Ornatoraphidia christianodagmara* (Euboea), *Ph. (Superboraphidia) minois* (Crete), and particularly *Subilla principiae* (Sardinia). This latter species has so far only been found in a small light forest of *Quercus pubescens*.

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